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Population Dynamics and Ecology of Beach Wrack Macroinvertebrates of the Central California Coast

Derrick R. Lavoie

Abstract.—Population dynamics and ecology of beach wrack macroinvertebrates of the central California coast by Derrick R. Lavoie, *Bull. Southern California Acad. Sci.*, 84(1):1-22, 1985. The successional cycle of macroinvertebrates colonizing high intertidal beach wrack islands, decaying clumps of stranded kelp, were examined on a central California high energy beach. Samples from wrack algae and the underlying sand were taken at periodic intervals following island deposition. Mean density and number of different species fluctuated in regular and complementary patterns. Multivariate analysis distinguished early, mid, and late colonizing species. Dipterans and amphipods were initial colonizers succeeded largely by Coleoptera. Temporal changes in faunal populations are attributed to physical and biological factors degrading the wrack and reducing its potential as a resource. Beach wrack is a major nutrient source and substrate shelter for a majority of indigenous beach fauna.

The sandy marine beach supports a large variety of macroinvertebrates primarily associated with decaying organic debris or beach wrack (Yaninek 1980). Marine macrophytes, deposited on the beach in discrete clumps or islands, are the major wrack source. Wrack islands provide beach fauna with nutrients, shelter, and a hospitable environment for reproduction and growth. Amphipods account for the greatest biomass, dipterans are most abundant, and coleopterans most diverse (Yaninek 1980). Additional constituents include pseudoscorpions, isopods, centipedes, spiders, mites, collembolans (Moore and Legner 1974a), and a microfauna of protozoa and bacteria (Eltringham 1971). High beach wrack is a limiting resource due to rapid algal decay, consumption, and environmental disturbances responsible for its degradation (Yaninek and Pitelka 1979). Ultimately, periodic wrack deposition is essential for the maintenance, and perhaps the very existence, of an indigenous shore community.

Previous studies of the ecology of beach wrack have largely concentrated on the natural history of individual macroinvertebrate taxa. Bowers (1964) and Hayes (1974) studied amphipods and isopods, respectively, Egglishaw (1960), Dobson (1974), and Poinar (1977) seaweed flies, and Moore and Legner (1976) beetles. Others have examined the general ecology of beach wrack (Backlund 1945; Dahl 1952; Eltringham 1971; Pearse et al. 1942; Steele and Baird 1968), and species distributions (Craig 1970; Fawcett 1969). Few considered wrack faunal succession (Griffiths and Stenton-Dozey 1981; Moore and Legner 1974b; Yaninek 1980).

This paper describes successional changes in the numbers and densities of macroinvertebrate species from selected high beach wrack islands. Beach wrack community structure and its relative importance to the shore ecosystem is discussed.

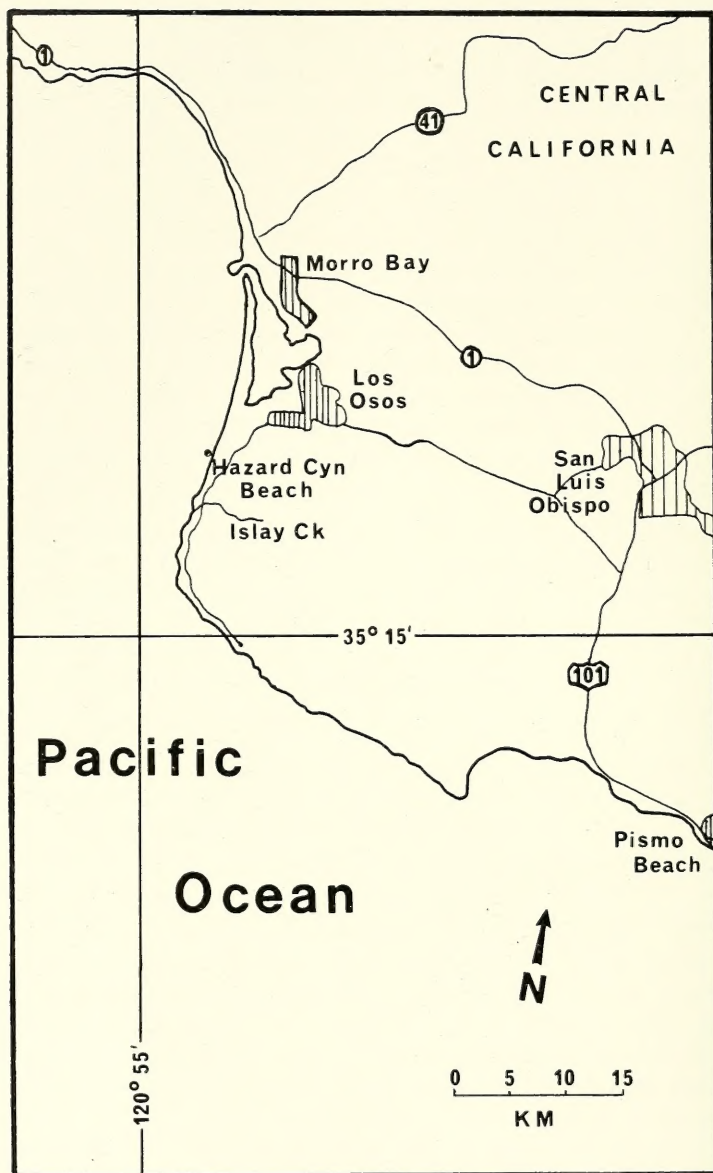


Fig. 1. Map of the central California coastal region showing the location of the study site at Hazard Canyon Beach, San Luis Obispo county.

Methods

The Study Area

One kilometer of shoreline at Hazard Canyon Beach, San Luis Obispo county ($123^{\circ}50'N$ by $35^{\circ}08'W$) was selected as the study site (Fig. 1). Being an open coast high energy beach, Hazard Canyon Beach receives full wave exposure. The beach, composed of fine-grained quartz sand (median particle diameter $400\ \mu m$), follows a sharp acclivity from low to mid tidal level (beach slope ratio $\frac{1}{6}$) becoming a gently sloping berm for approximately 20 m into the high tide zone (slope $\frac{1}{25}$). It is backed by steep sand cliffs supporting a dune floral community of such species

as *Artemisia pycnocephala*, *Franseria chamissonis*, *Lathyrus littoralis*, *Lupinus arboreus*, and *Abronia maritima* (Munz and Keck 1968).

Sampling

Temporal changes of high intertidal beach wrack faunal populations were examined for an 80 day period from 21 June to 10 Sept. 1981. Five wrack island cohorts, each consisting of five wrack islands of similar size, algal composition, tidal height, and proximity (within 5 m of each other) were sampled at 2–4 day intervals following initial deposition on the high beach, and thereafter, at about weekly intervals throughout each island's life. New cohorts were selected from kelp deposited during the high-high spring tides. For each sampling period a sand and wrack sample were taken from one of seven randomly chosen positions of each cohort island. Since each island was roughly rectangular, island volume was calculated from measurements of island length, width, and height obtained using a meter cord. A sand sample consisted of an $\frac{1}{8}$ by $\frac{1}{8}$ m area of surface layer sand cored to a depth of 15 cm beneath a wrack island. A wrack sample constituted approximately $\frac{1}{8}$ by $\frac{1}{8}$ m area of semi-compacted seaweed cored directly above a sand sample.

On the beach, the "bucket flotation technique" was used to separate organisms from each sample. Sand or wrack algae were lowered into a bucket of sea water causing adult, pupal, and larval macroinvertebrates to float to the surface. They were then dip-netted and preserved directly in 70% ethanol. In the laboratory, organisms were separated into species groups, counted, assigned numbers for easier reference, and usually identified to species using standard keys (Borror et al. 1981; Doyen 1976; Evans 1980; Moore and Legner 1976). Unidentified species were submitted to taxonomic specialists (Doyen, per. comm.; Schlinger, per. comm.).

Due to the tendency for adult Diptera to fly away, and amphipods to sink in the collection bucket, early colonization of wrack by these forms was quantified with "sticky traps." Traps were circular plastic plates (0.1 m in diameter) smeared with "tangle-foot" (Tangle-foot Company, Grand Rapids, Michigan). Three identical wrack islands (initial volume = 0.5 mm), newly deposited in the high intertidal, where inundation was not a factor, were sampled beginning at 0600 at 12, 24, 36, 48, 72, 96, 120, and 148 hour intervals. The numbers of each species were recorded at respective intervals and new traps replaced. Each island was sampled with six replicate traps: two placed on the island near its center ("on wrack"), and four evenly spaced adjacent to its perimeter on the sand ("on sand").

Data Analysis

Species counts were subjected to analysis of variance (ANOVA) and *t*-tests (prob. $H_0: \bar{x}_{\text{sand}} = \bar{x}_{\text{wrack}}$) to determine any significant differences between and within sampling positions of each cohort. To describe variations of species between cohorts, similarity correlations were calculated for all possible binary combinations using Dice's Similarity Coefficient (Pielou 1977):

$$\text{DSC} = \frac{2(A \cup B)}{(A + B)}$$

$A \cup B$ = # of species common to both cohorts
 A = # of species found in cohort A
 B = # of species found in cohort B

Unity indicates perfect correlation.

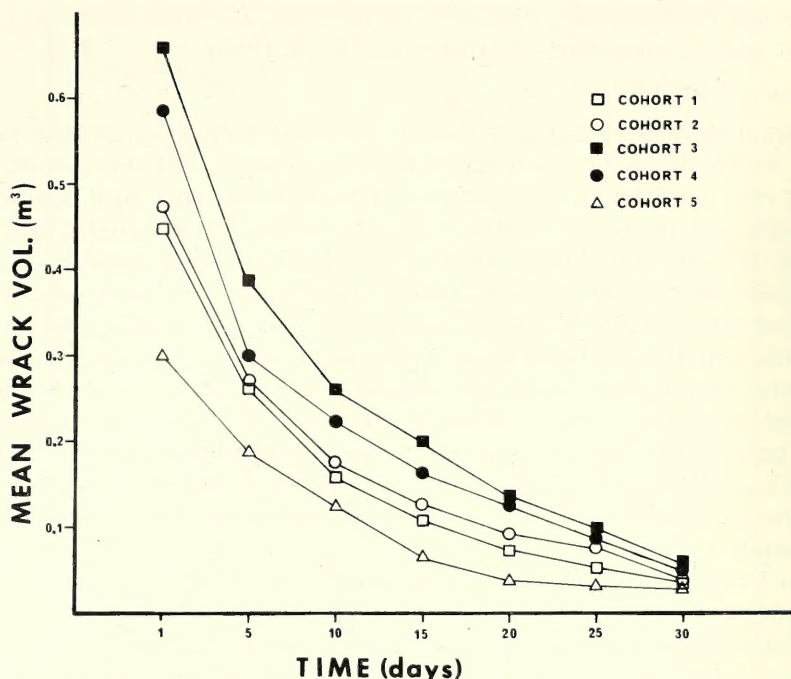


Fig. 2. Mean change in wrack volume throughout the sampling period for cohort's one through five.

Reciprocal averaging (RAVG) was used to provide a clearer representation (i.e., separation) of the successional stages by which shore macroinvertebrates colonize beach wrack. RAVG is a multivariate ordination technique utilizing presence-absence data to describe a community in terms of an environmental gradient. It iterates species scores (present = 1; absent = 0) and site scores (survey site 1 to n) to obtain the distribution of species conforming to a site gradient (Pimentel 1979). In this study the site scores become sampling periods thereby making the site gradient the successional trend through time. Species occurring more than once in all islands of a cohort for a given sampling period were considered as "residents." Only these species were used in the data analyses.

Results

Hazard Canyon Beach received an ample supply of deposited wrack algae, mainly *Macrocystis pyrifera*, *Nereocystis luetkeana*, and *Egregia menziesii*, during the sampling period. Wrack islands were typically deposited in localized groups of 10 to 15 islands (approximately 1–2 m in diameter) along relatively narrow sections of coastline (less than 50 m). *Zostera marina* strand occurred intermittently around and on unselected wrack islands.

The texture and pigment conditions of the selected high beach wrack island kelp cohorts followed a typical decay sequence. Upon deposition they were dark brown, moist, and flexible, then gradually became wrinkled, less flexible and often

Table 1. Taxonomically categorized species list of macroinvertebrates collected from selected beach wrack cohorts during the study period. Unspecified species are adult forms. Reference numbers used for initial identification and computer analyses are shown. Asterisks indicate resident species.

Taxa	Reference number
ARACHNIDA	
Acarina (mites)	
Bdellidae	
<i>Neomolgus</i> sp.	T-21*
Unidentified sp.	T-89
Araneae (Spiders)	
<i>Spirembolus mundus</i> Chamberlin	T-25
Pseudoscorpionida (pseudoscorpions)	
Garypidae	
<i>Garypus californicus</i> Banks	T-41*
CHILOPODA	
Geophilomorpha (centipedes)	
Schendylidae	
<i>Nyctunguis heathii</i> Chamberlin	T-23*
CRUSTACEA	
Amphipoda (beach hoppers)	
Talitridae	
<i>Orchestoidea benedicti</i> Shoemaker	T-33*
<i>Orchestoidea californiana</i> Brandt	T-32*
Isopoda (pill bugs)	
Oniscidae	
<i>Alloniscus perconvexus</i> Dana	T-63
<i>Tylos</i> sp.	T-84
Unidentified sp.	T-60
INSECTA	
Coleoptera (beetles)	
Anabidae	
Unidentified sp.	T-80
Anthicidae	
<i>Amblyderus obesus</i> Casey	T-95
Carabidae	
<i>Anisodactylus californicus</i> (larvae) Dejong	T-58
<i>Trechus ovipennis</i> Mutschulsky	T-19
Curculionidae	
<i>Curculio</i> sp.	T-42
<i>Emphyastes fucicola</i> Mannerheim	T-22
Histeridae	
<i>Bacckmenniulus gandens</i> LeConte	T-39*
<i>Euspilotus scissus</i> LeConte	T-37*
<i>Hypocaccus bigemminus</i> LeConte	T-36*
<i>Neopachylopus</i> sp.	T-48
Unidentified larvae	T-55
Hydrophilidae	
<i>Cercyon luniger</i> Mannerheim	T-6*

Table 1. Continued.

Taxa	Reference number
Unidentified larvae	T-46
Limnebiidae	
<i>Octhebius rectua</i> LeConte	T-8
Melyridae	
<i>Endeodes basilis</i> LeConte	T-66
<i>Endeodes basilis</i> (larvae)	T-91
Mordellidae	
<i>Mordella marginata</i> Melsheimer	T-52
Nitidulidae	
<i>Carpophilus</i> sp.	T-93
Rhizophagidae	
<i>Phyconomus marinus</i> LeConte	T-11*
Salpingidae	
<i>Aegialites</i> sp.	T-20
Staphylinidae	
<i>Aleochara sulcicolis</i> Mannerheim	T-3*
<i>Aleochara</i> sp.	T-17
<i>Bledius monstratus</i> Casey	T-1*
<i>Cafius canescens</i> Maklin	T-2*
<i>Cafius luteipennis</i> Horn	T-16*
<i>Hadrotus crassus</i> Mannerheim	T-81
<i>Omalium algarum</i> Casey	T-96
<i>Pontomalota</i> sp.	T-14
<i>Proteinus</i> sp.	T-18
<i>Tarphiota geniculata</i> Maklin	T-4*
<i>Tarphiota pallidipes</i> Casey	T-5*
<i>Thinopinus pictus</i> LeConte	T-10
<i>Thinusa maritima</i> Casey	T-15
Unidentified larvae	T-65*
Unidentified pupae	T-92
Tenebrionidae	
<i>Eleodes</i> sp. (larvae)	T-28
<i>Phaleria rotundata</i> LeConte	T-73*
<i>Phaleria rotundata</i> (larvae)	T-29
Diptera (flies)	
Anthomyiidae	
<i>Fucellia costallis</i> Stein	T-40*
<i>Fucellia costallis</i> (larvae)	T-45*
<i>Fucellia costallis</i> (pupae)	T-50
Coelopidae	
<i>Coelopa vanduzeei</i> Cresson	T-30*
<i>Coelopa vanduzeei</i> (larvae)	T-64*
Milichiidae	
<i>Neophyllomyza</i> sp.	T-61
Sphaeroceridae	
<i>Copromyza atra</i> Meigen	T-43*
<i>Copromyza atra</i> (larvae)	T-47*
<i>Copromyza atra</i> (pupae)	T-49*
Unidentified eggs (T-30, T-40, T-43)	T-62*

Table 1. Continued.

Taxa	Reference number
Hymenoptera (bees and wasps)	
Ceratinidae	
<i>Ceratina</i> sp.	T-77
Chrysomelidae	
Unidentified sp.	T-24
Pteromalidae	
Unidentified sp.	T-79
Vespidae	
Unidentified sp.	T-12
Orthoptera (grass-hoppers, etc.)	
Gryllidae	
Unidentified sp.	T-82
Gryllacrididae	
Stenopelmatinae	
Unidentified sp.	T-75
Mantidae	
<i>Stagmomantis</i> sp.	T-76
NEMOTADA (pin worms)	
Unidentified sp.	T-44*

bleached lighter by the sun. Island volume (biomass) declined initially (one to five days) at a relatively rapid rate, then slowed to a low and steady loss through late succession (30 + days, Fig. 2). Although the interiors of each island retained the greatest amount of moisture, they eventually dried out completely to be blown away by wind, washed back out to sea, or further buried by sand.

Faunal Composition

Fifty-three species of macroinvertebrates comprising five classes, 12 orders, and 32 families were collected from selected wrack islands of the high intertidal (Table 1). The tidal heights of the cohorts and their collection dates are given in Table 2. The Coleoptera were most diverse, represented by 14 families, with over half of the species in the family Staphylinidae. Twenty-seven species of adult, larval, egg, or pupal stages were distinguished as residents. In all cases, except for dipteran pupae, unidentified taxa represent only a single species. Furthermore, in the cases involving only one adult and one unidentified larva (e.g., T-6, T-46) I strongly suspect the larvae to be the same species as the adults.

Faunal Succession

The succession of wrack invertebrates followed a characteristic pattern as revealed by RAVG multivariate analysis of combined sand and wrack presence-absence data. Species plots for each cohort separated resident species into three main areas which I have designated early (E), mid (M), and late (L) successional periods (Fig. 3). Site plots (i.e., sampling periods) reflect this species pattern

Table 2. Sampling periods and intertidal beach deposition height above MLLW for all cohorts.

	Sampling dates							Tidal height ft.
	1	2	3	4	5	6	7	
Cohort 1	6/23	6/25	7/2	7/9	7/15	7/22	7/28	7.0
Cohort 2	7/23	7/25	8/2	8/10	8/18	8/25	8/31	6.8
Cohort 3	8/19	8/21	8/25	8/31	9/6	9/14	9/22	7.3
Cohort 4	9/5	9/7	9/11	9/17	9/25	10/3	10/7	6.5
Cohort 5	9/16	9/18	9/26	10/3	10/10	10/15	10/22	6.4

showing good distinction between successional periods (Fig. 4). In general, early colonizers were adult diptera (*Coelopa vanduzeei*, T-30; *Fucellia costallis*, T-40; *Copromyza atra*, T-43) and amphipods (*Orchestoidea californiana*, T-32; *Orchestoidea benedicti*, T-33) as indicated by RAVG species plots and sticky trap data (Figs. 5 and 6). Diptera eggs (T-62) of at least two distinguishable sizes (approximately 2 mm and 4 mm) were also laid during this period. After raising some of these eggs to larvae, I found the small eggs to be *Copromyza atra*, and the large eggs to be either *Coelopa vanduzeei* or *Fucellia costallis*.

The pattern of early colonization determined by sticky traps was similar in both "on sand" and "on wrack" samples, but greater numbers of individuals were captured on the wrack samples and two more species were found on the sand samples. No significant differences were evident between the replicates of each sampling position (ANOVA: P -values $> 0.05\%$). Wind was negligible during the sticky trap sampling period.

Early successional species declined after about a week to be replaced by a large variety of mid successional forms (Fig. 3), dominated by staphylinid beetles (e.g., *Cafius canescens*, T-2; *Aleochara gulcicolis*, T-3; *Tarphiota geniculata*, T-4) and fly larvae (*Coelopa vanduzeei*, T-64; *Copromyza atra*, T-47, *Fucellia costallis*, T-45). Mites (*Neomolgus* sp., T-21), pseudoscorpions (*Garypus californicus*, T-41), and several other beetle families (Rhizophagidae, T-11; Histeridae, T-36 and T-37; Hydrophilidae, T-6) also established this stage. Later successional species were commonly adult terrestrial tenebrionids (T-35) and histerids (T-36 and T-39). In addition, Diptera pupae (T-49 and T-50) were regularly present during late succession, and in some cases *Fucellia costallis* larvae, T-45 (see cohort one and five, Fig. 4).

Diversity and Density

Total mean densities for combined species (grand totals), not including adult Diptera or Amphipoda, varied widely between cohorts with cohort three exhibiting a markedly higher density (Table 3). Greater population totals were evident in sand samples for cohort one and two, but in wrack samples for the other cohorts. None of the t -tests comparing sampling positions within cohorts were significant ($0.1 > P$ -value $> 0.05\%$, Table 3). Moreover, one-way ANOVAs revealed no significant differences (P -values $\gg 0.05\%$) among either sand or wrack replicate island samples for each cohort (Table 4).

Fluctuations of resident species were similar for sand or wrack samples of all

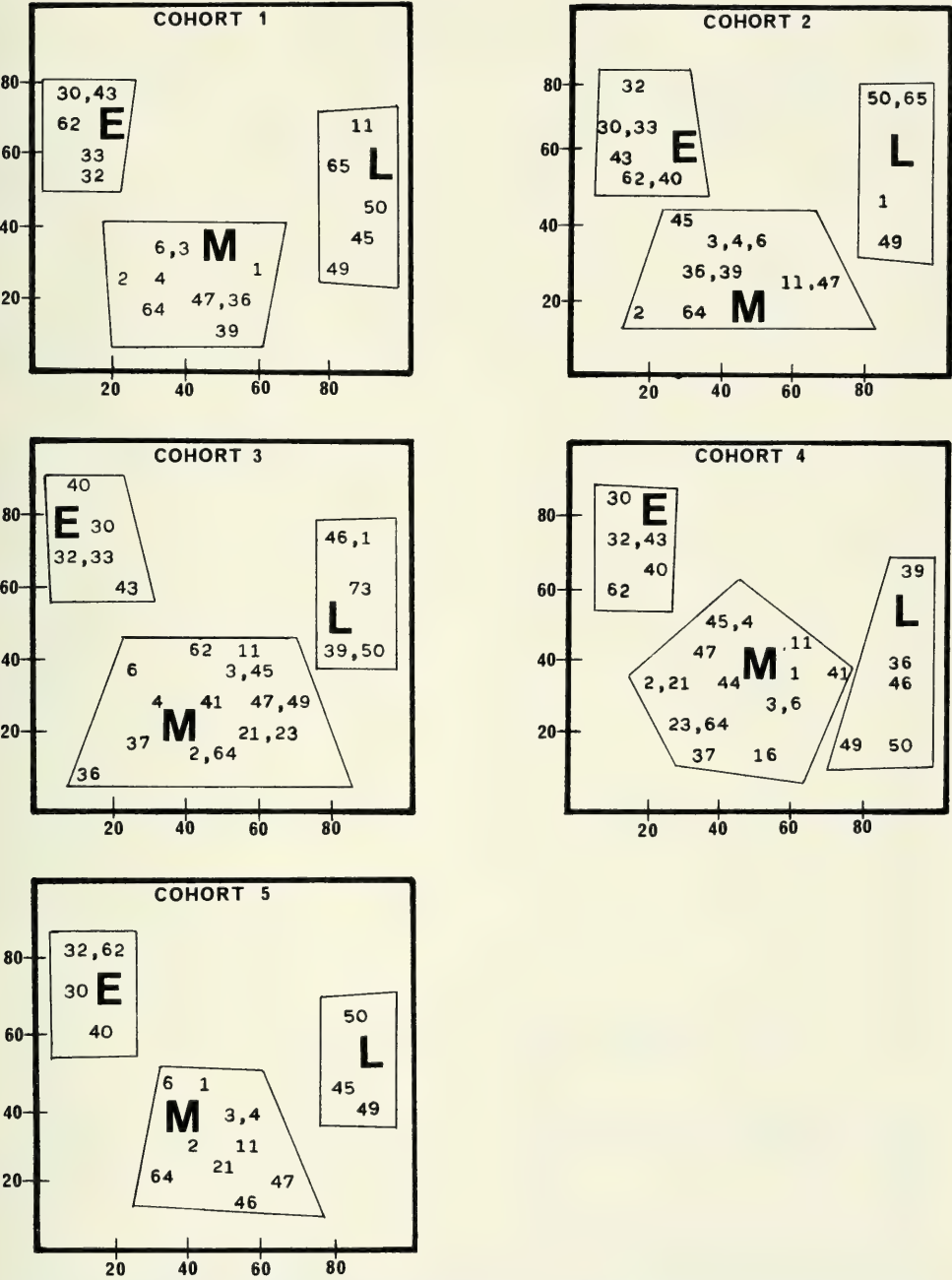


Fig. 3. Reciprocal averaging (RAVG) species plots of combined sand and wrack sampling position presence-absence data for resident species throughout the sampling period of each cohort. Numbers correspond to species classified as early (E), mid (M), or late (L) successional. Abcissa = first axis; ordinate = second axis.

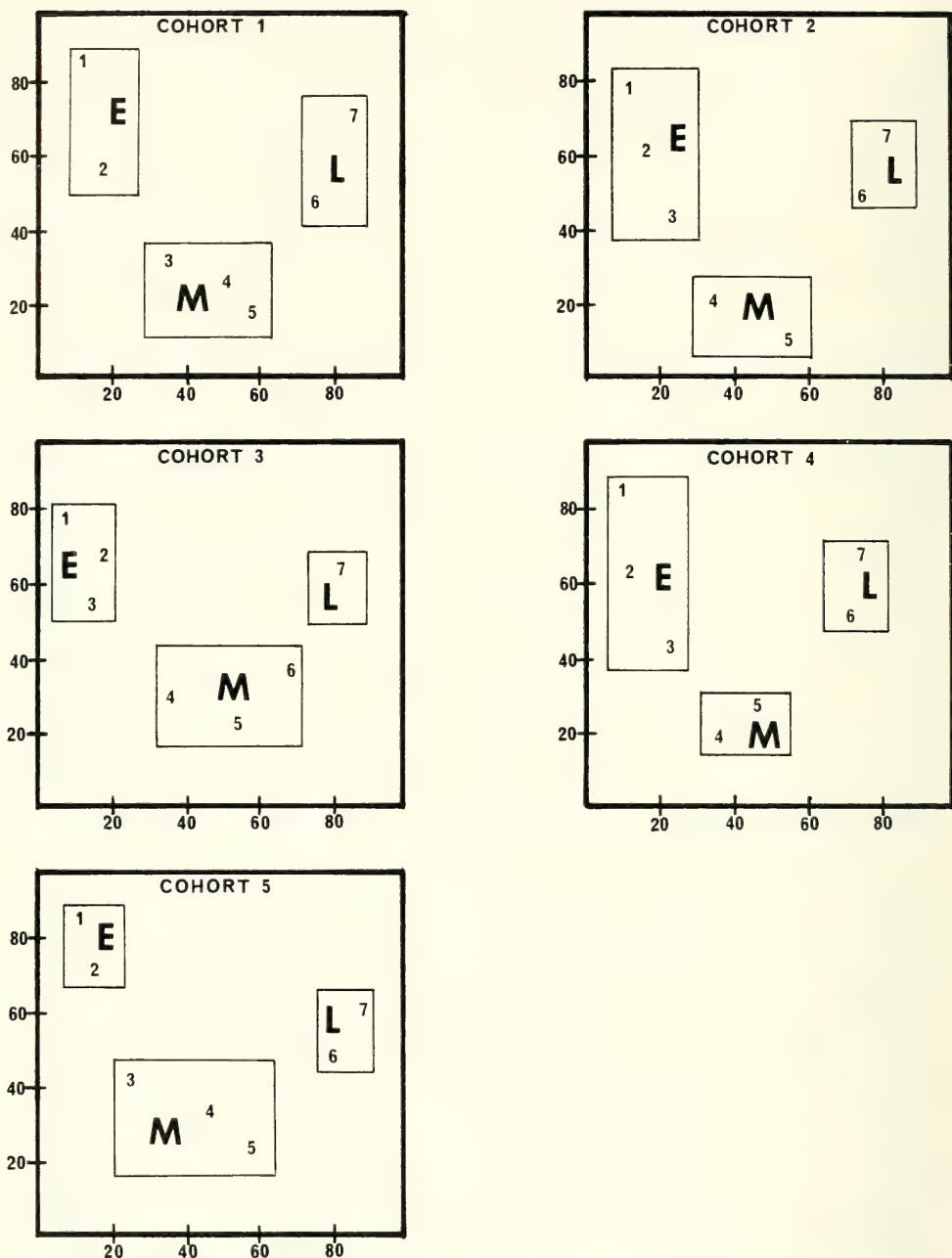


Fig. 4. Reciprocal averaging (RAVG) site plots of combined sand and wrack sampling position presence-absence data for resident species throughout the sampling period of each cohort. Numbers correspond to sampling periods. Abcissa = first axis; ordinate = second axis.

cohorts (Fig. 7). Numbers of wrack species always increased relatively rapidly for the first few days following algae deposition (early succession), peaked for a few days during mid succession (two to three weeks), then gradually decreased through

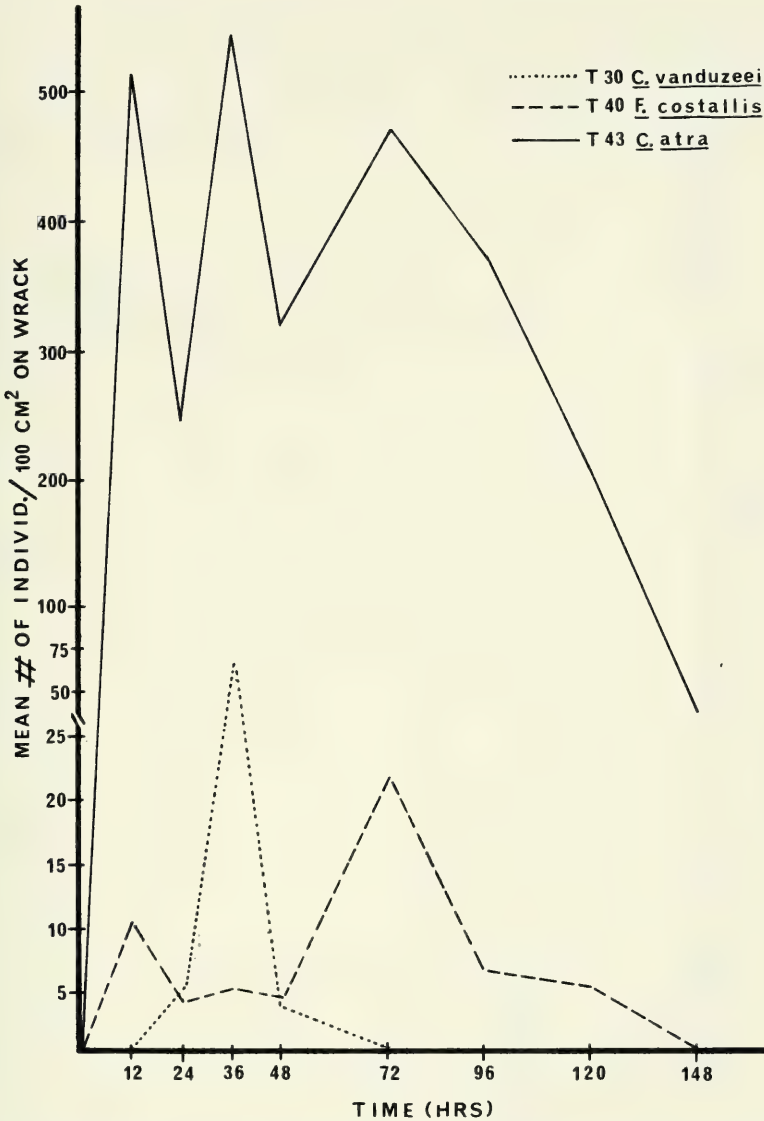


Fig. 5. Mean number of adult dipterans (T-30, T-40, T-43) caught with sticky trap "on sand" samples for 148 hours following wrack island deposition (three islands, four replicates, N = 12).

late succession (four to five weeks). Numbers of sand species increased more slowly than wrack species during early succession, stabilized at a higher relative maximum during later mid succession, then decreased rather quickly thereafter. At late succession, sand species were always greater than wrack species. Dice's Similarity Coefficient disclosed a high correlation between all binary cohorts, with cohort one and two having identical resident species (Table 5).

Mean density changes of all resident species combined (minus adult Diptera and Amphipoda) were also similar for either sand or wrack samples of all cohorts (Fig. 8). Wrack densities commonly increased rapidly to attain maximum values

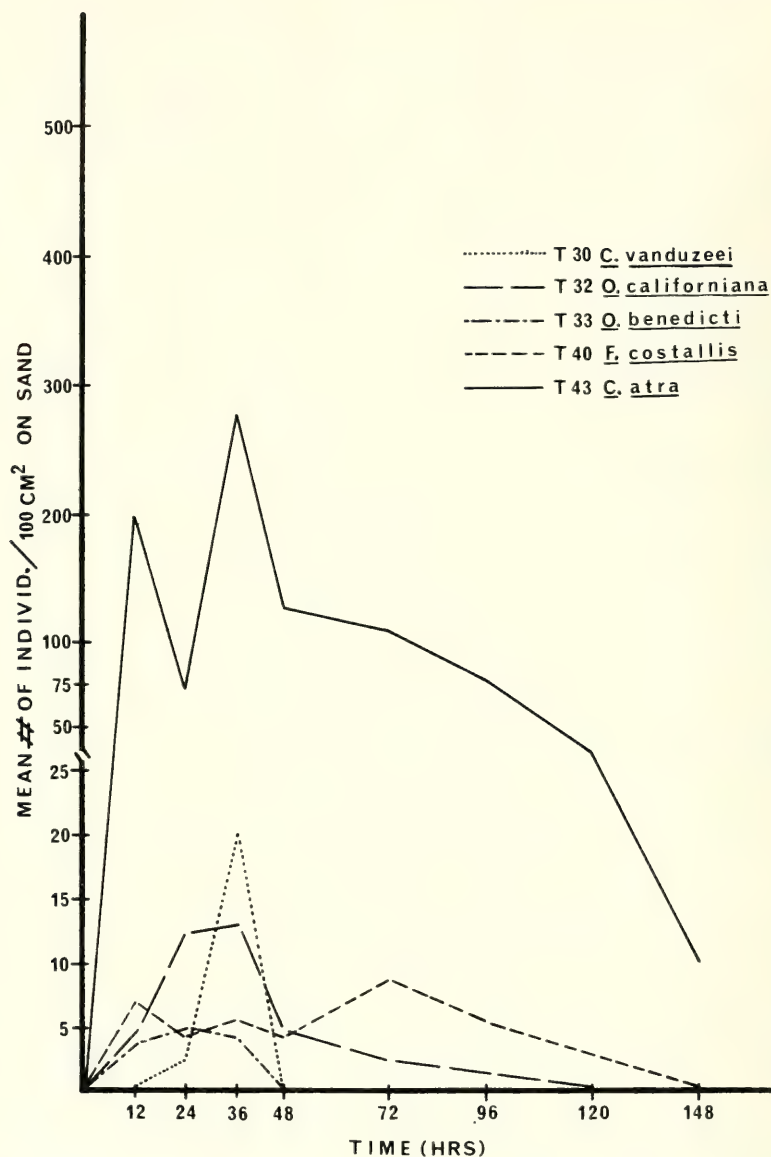


Fig. 6. Mean number of amphipods (T-32, T-33) and adult dipterans (T-30, T-40, T-43) caught with sticky trap "on wrack" samples for 148 hours following wrack island deposition (three islands, two replicates, $N = 6$).

during early-mid succession, then gradually decreased to lower values by late succession. Sand densities increased more gradually during early succession, peaked by mid-late succession, then decreased relatively quickly.

Discussion

Open sandy beaches support an abundant, stable, and diverse meiofauna (McIntyre 1968; McLachlan 1977a), but generally sustain a relatively impoverished macrofauna (Eltringham 1971; McLachlan 1977b). However, following de-

Table 3. Mean number of resident species per $\frac{1}{64}$ m² collected from sand (S) and wrack (W) sampling positions for each cohort overall sampling periods. Reference numbers and common names of each taxon identify species which are adult species unless specified as larval (L), pupal (P), or egg (E) forms. Sand, wrack, and grand totals are computed for each cohort, and *t*-tests compare sampling positions within each cohort. Amphipods and adult Diptera are not included due to inappropriate sampling technique. NS = number of resident species per cohort, n = number of sampling periods.

Common name of taxon	Ref. num.	Cohorts									
		1		2		3		4		5	
		NS = 15 n = 7		NS = 15 n = 7		NS = 20 n = 7		NS = 21 n = 7		NS = 14 n = 7	
		S	W	S	W	S	W	S	W	S	W
Beetle	T-1	15	5	15	8	6	3	85	36	9	2
Beetle	T-2	25	16	20	13	6	5	11	4	39	25
Beetle	T-3	25	35	34	144	95	171	100	114	75	71
Beetle	T-4	62	18	68	28	66	24	60	52	12	4
Beetle	T-6	133	220	52	121	20	75	111	379	93	197
Beetle	T-11	375	140	272	159	740	280	55	35	18	14
Beetle	T-16	0	0	0	0	0	0	3	15	0	0
Mite	T-21	0	0	0	0	13	22	12	28	16	30
Centipede	T-23	0	0	0	0	8	3	18	10	0	0
Beetle	T-36	22	7	28	5	9	3	12	6	0	0
Beetle	T-37	0	0	0	0	8	8	22	8	0	0
Beetle	T-39	185	25	192	32	182	83	115	9	0	0
Pseudosc.	T-41	0	0	0	0	42	31	11	11	0	0
Nematode	T-44	0	0	0	0	0	0	10	29	0	0
Fly (L)	T-45	125	230	32	243	430	1450	151	310	155	345
Beetle (L)	T-46	0	0	0	0	32	25	48	28	197	88
Fly (L)	T-47	322	151	380	145	110	355	77	23	369	144
Fly (P)	T-49	620	180	750	219	510	202	513	252	410	140
Fly (P)	T-50	32	8	133	18	28	10	92	33	16	4
Fly (E)	T-62	230	570	210	518	80	145	210	680	205	495
Fly (L)	T-64	13	27	25	109	26	102	110	426	108	329
Beetle (L)	T-65	10	15	8	24	0	0	0	0	0	0
Beetle	T-73	0	0	0	0	10	39	0	0	0	0
Total		2194	1647	2219	1786	2421	3036	1826	2488	1722	1888
Grand total		3841		4005		5457		4314		3610	
<i>t</i> -value		0.055		0.068		0.073		0.051		0.085	

position of kelp wrack on the high shore, this study has shown that populations of macroinvertebrates increase markedly in abundance and diversity. Wrack faunal succession exhibited three distinguishable stages in all five sampled cohorts implying a regular and predictable sequence. Early successional species were flies and amphipods, replaced by a wide variety of mid successional forms (coleopterans, pseudoscorpions, isopods, mites, etc.), eventually succeeded by more terrestrial late successional Coleoptera. The high beach wrack successional cycle is curtailed by physical and biological factors which eventually limit the wrack resource.

Physical Factors

The amount of algae deposited on the beach increases with seasonal storms or high swell activity (Neushul 1967; ZoBell 1971). The kelps, having large surface

Table 4. One-way analyses of variance comparing mean number of resident species from sand or wrack sampling positions between all sampling periods for each cohort (N = 5). *P*-value $\geq$ 0.05% in all cases.

Source of variation	ANOVA			
	df	SS	MS	F
Cohort 1 wrack	4	2374.658	593.644	1.324
Error	70	31,387.097	448.389	
Total	74	33,761.755		
Cohort 2 wrack	4	1619.396	404.849	0.767
Error	70	36,948.415	527.835	
Total	74	38,567.811		
Cohort 3 wrack	4	4614.347	1153.587	1.465
Error	95	74,805.964	787.431	
Total	99	79,420.310		
Cohort 4 wrack	4	3140.792	785.198	1.337
Error	100	61,664.768	587.283	
Total	104	64,805.560		
Cohort 5 wrack	4	1153.713	288.428	0.731
Error	65	25,646.828	394.566	
Total	69	26,800.540		
Cohort 1 sand	4	2773.787	693.447	1.783
Error	70	27,224.491	388.921	
Total	74	29,998.277		
Cohort 2 sand	4	1530.120	382.830	0.892
Error	70	30,019.171	428.845	
Total	74	31,549.291		
Cohort 3 sand	4	7524.334	1881.108	2.234
Error	95	79,993.420	842.036	
Total	99	87,517.753		
Cohort 4 sand	4	1836.354	459.885	0.666
Error	100	72,378.821	689.322	
Total	104	74,215.175		
Cohort 5 sand	4	2208.913	552.228	1.334
Error	65	26,907.673	413.964	
Total	69	29,116.586		

areas and a tendency to float on or near the water's surface, are likely to uproot and drift. Depending on local currents and the wind, kelp rafts may be stranded on a sandy shore. By combining knowledge of such physical parameters with the location of offshore kelp beds a general prediction of the seasonal quantity of wrack deposited on any given beach should be possible. *Prima facie*, long beaches with wide berms provide greater surface area and potentially receive the most wrack.

Persistence of wrack on the shore depends on intertidal island position and the rate of algal degradation. Three subzones based on the reach of the tides and the lag time following deposition can be recognized (slightly modified from Moore and Legner 1974a):

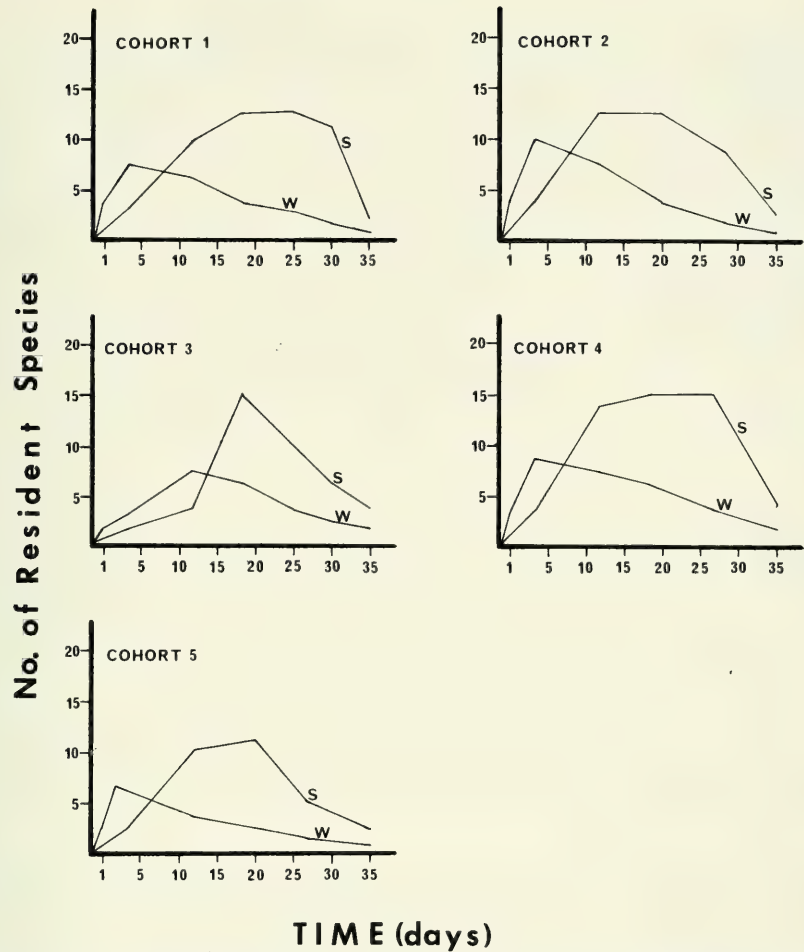


Fig. 7. Numbers of resident species from sand (S) and wrack (W) sampling positions throughout the sampling period for each cohort.

- 1). Area of fresh seaweed (left for one to three days, 4 ft tide level).
- 2). Area of decaying seaweed, wetted by occasional high tides (left for 4–15 days, 6 ft tide level).
- 3). Area of dry seaweed, wetted only by the highest tides of the month (left for 15+ days, 7 ft tide level).

Table 5. Dice's similarity correlation coefficients for all binary combinations between all cohorts. Unity indicates perfect correlation and identical species diversities.

	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5
Cohort 1	1.00	1.00	0.76	0.77	0.80
Cohort 2		1.00	0.76	0.77	0.80
Cohort 3			1.00	0.85	0.82
Cohort 4				1.00	0.83
Cohort 5					1.00

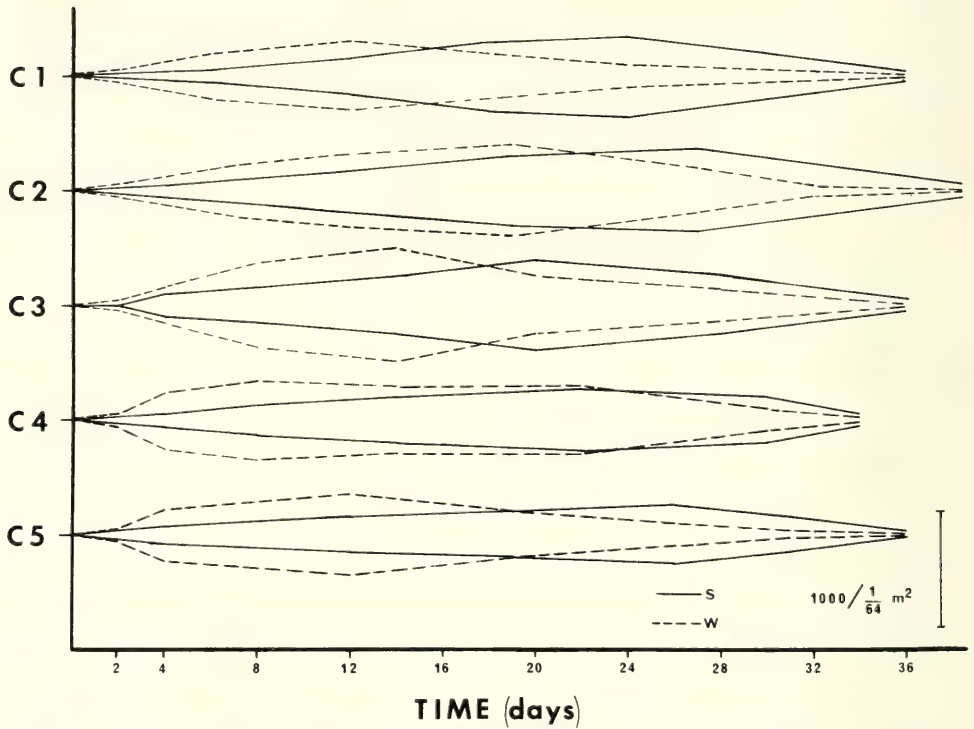


Fig. 8. Mean densities of combined resident species per $\frac{1}{64} \text{ m}^2$ from sand (S) and wrack (W) sampling positions throughout the sampling period for each cohort.

The pattern of succession described by this study for high beach wrack (subzone three) may be quite different for lower intertidal wrack since each subzone supports characteristic macroinvertebrates (Moore and Legner 1974b). Tidal submergence of wrack may prolong island life by adding moisture and perhaps replenishing nutrients (e.g., bacteria, surf plankton) needed for faunal growth and reproduction. However, it may push back the successional cycle by driving out several vulnerable wrack residents. Parenthetically, an island may be washed back out to sea, repositioned on the beach, or further buried by sand following inundation. It is plausible that the original island deposition site is quite stable. Yaninek and Pitelka (1979) found some wrack islands remained in their originally deposited positions for up to 140 days, and Lavoie (1982) determined the location of reinundated islands to be relatively unaffected by rising tides. Undoubtedly, wave action and wind intersperses sand between the stipes of the kelps to establish an effective anchor for the entire island.

Sun and wind dry out the wrack, reduce its suitability as a resource, and thereby stunt the successional cycle. The desiccation sequence, which followed moisture loss from the outside toward the wrack's interior, could largely account for increasing densities and diversities of sand positions towards later succession (Figs. 7 and 8). I suspect moisture is an essential requirement for a majority of the wrack constituents.

The fact that the larger volume cohorts supported a progressively greater variety

and quantity of macroinvertebrates (correlation coefficient $r = 0.871$; P -value $< 0.05\%$: see Table 3 and Fig. 2) suggest a species-area relationship (Conner and McCoy 1979; MacArthur and Wilson 1967; Preston 1960). Larger islands requiring a longer time to desiccate and decay offer greater stability, added habitat, and more potential food. Additionally, larger islands should more effectively reach higher interior decay temperatures and reduce developmental times of egg and pupal stages (Poinar 1977). However, time of development may be based more on the frequency of inundation as determined by the tidal height of islands up the shore. Kompfner (1974) postulated high beach wrack larvae and pupae have longer developmental periods than species of lower beach wrack. It follows, the maturation time of given beach residents required to achieve successful reproduction must be less than the life of the chosen "home" island. For some species (particularly larval stages) maturation probably must occur before the detrimental effects of the rising tides (Yaninek 1980).

Biological Factors

Species interactions, patchiness, variable feeding, dispersal, reproductive rates, and even inhibitory effects may affect the successional cycle of high beach wrack organisms. Initial consumption of kelp by amphipods (Griffiths and Stenton-Dozey 1981) and subsequent feeding by dipteran larvae may severely deplete wrack biomass. Perhaps, initial colonizers establish physiological conditions required by mid successional species which, in turn, modify the substrate for later forms. Egglshaw (1960) noticed feeding larvae greatly enhanced wrack decomposition and Rowell (1969) found certain sandy beach organisms have food requirements dependent upon bacterial synthesis. Connell and Slatyer (1977) criticize such a "facilitation model" and favor an "inhibition model" whereby early colonists preempt space and resist invading competitors until they die and release the resource to their successors. Although data for other systems are largely consonant with the "inhibition model" (Lubchenco and Menge 1978; Souza 1979), it seems an alternative "tolerance model" better describes wrack succession. This latter hypothesis accounts for a predictable sequence resulting from differing adaptations of early, mid, or late successional species (Stearns 1982). For example, adult flies and amphipods, which require highly moist environments for feeding on mucous and laying eggs, decline after a week or so as the wrack dries out and more tolerant mid successional forms invade the wrack, which then are replaced by even more desiccation resistant or terrestrially adapted species. Thus, the physical degradation of wrack by environmental factors alone may determine the physiological tolerances that select for given constituents.

Patchiness may result from beach species congregating at localized wrack cohorts, randomly distributed along the shore. Perhaps this explains the much higher abundance of *Coelopa vanduzeei* (T-30) and the coincident decrease in density for *Fucellia costalis* (T-40) on the second day (24–48 hours) of sticky trap sampling (Fig. 6). Patchiness may also arise from diurnal, nocturnal, and tidal biorhythms, quite common on the shore (Craig 1970; Evans 1976; Moore 1975). A diurnal rhythm seems evident for all three dipteran species during the first 48 hours of sticky trap sampling (Figs. 5 and 6), possibly due to decreased nighttime temperatures.

Organisms (e.g., flies and amphipods) most capable of long range dispersal

should colonize newly deposited wrack islands first. Although both visual and chemical cues may be utilized to locate any new islands the sticky trap data in this study did not detect a chemotactic response. Had there been a predominating wind and chemical dispersal the leeward replicate samples should have captured more individuals. The much higher densities obtained with the "on wrack" samples suggests macroinvertebrate orientation was visual.

Predators, scavengers, saprovores, herbivores, and detritivores constitute several dynamic trophic levels of the beach wrack community (Lavoie 1985). Undoubtedly, both intra and interspecific interactions involving predation, competition, and parasitism, influence the beach wrack community structure. A large number of predatory forms (Staphylinidae, Histeridae, Carabidae, and Hydrophilidae larvae) suggests the attainment of maximum diversity during mid succession can, in part, be explained by the "predation hypothesis" (Lubchenco 1978). Predators, by preventing competitive exclusion and high prey abundances, select for greater variety of species (Paine 1966). Orth and others (1977) contend that adult Staphylinidae have a substantial impact on the density of seaweed flies and posit the use of certain species for biological control of noxious beach Diptera. Additionally, the ecological impact of parasitic forms has not been adequately investigated, but may prove to be considerable. Backlund (1945) observed high population levels of parasitic Hymenoptera on Diptera pupae and adult stages, and Yaninek (1980) cited heavy infestations of phoretic mites on adults of *Coelopa vanduzeei* (T-30).

Larval monopolies, reported by Egglshaw (1960), Dobson (1974), and Yaninek (1980), may occur as early colonizers rapidly reproduce. The greater mean density of cohort three (Table 3), attributable to high numbers of *Copromyza atra* larva (T-47), seems to infer such a monopoly. However, since this effect did not reduce the number of different species or disrupt the characteristic pattern of succession, I suspect competitive exclusion is not an important selective pressure in this community. Although it is possible larger wrack island volumes would allow for effective monopolization.

Egglshaw (1960) postulates that larval populations may reduce species diversity through the release of inhibitory substances. *Zostera marina*, which is sometimes deposited concurrently with kelp, was determined by Harrison and Chan (1980) to inhibit the growth of decaying bacteria. Its presence could significantly alter brown kelp wrack succession and may explain the considerably higher macroinvertebrate densities reported in brown compared to green algae wrack (Dobson 1976, Yaninek 1980).

Ecological Implications

Throughout this investigation wrack was usually present within the study site, and often, in large quantities. The question arises: what would happen to the beach fauna, many of which are endemic, during a long absence of wrack deposition? Obviously, species capable of flight may disperse to nearby beaches. However, their movement may be impeded by rocky coastline or even the type of beach sand (e.g., coarse to fine). Lavoie (1981) found two species of *Bledius* (Staphylinidae) to be divided in range by fifteen miles of rugged coarse-grained beach of the Diablo Canyon region along the central California coast. It is also

possible that some forms burrow down into the sand and remain in a dormant or quiescent state until surface wrack is provided (Moore and Legner 1974a). Kompfner (1974) found larvae to survive for several weeks by burrowing into the sand. This strategy should select for longevity rather than quick reproductions. Theoretically, as decimated wrack becomes buried in the higher shore regions it establishes a below-sand detrital based community. Here macroinvertebrates might seek refuge, albeit at relatively low levels, during paucity of new wrack. At this stage further decomposition and consumption by infaunal species probably ensues. Eventually the degraded organic wrack debris is washed back into the marine system where it may supply an important and direct nutrient source to detritus feeding organisms (Griffiths and Stenton-Dozey 1981) and even surf phytoplankton blooms (McLachlan and Lewin 1981). McLachlan (1981) contends surf phytoplankton to be a major food source of intertidal macrofauna filter feeders. In perspective, the presence of kelp wrack on the shore may have far reaching implications to the well being of the sandy beach and adjacent marine ecosystems.

Ostensibly, beach organisms must be hardy to survive in the harsh and limiting environment of the shore. But, how adaptable are they to environmental catastrophe? For instance, in the unfortunate event of a major oil spill or toxic pollutant discharge would beach species be endangered? It is probable that beach fauna are severely impacted by oil, which often accumulates on the shore (Mann and Clark 1978). Acting like sponges, wrack islands could retain heavy fractions of oil and become unsuitable for life support and colonization. An absence of *Thalassotrechus barbara* (Carabidae) along several beaches following the 1969 Santa Barbara oil spill supports this contention (Evans 1970). Evans (1970) found the hydrofuge properties of wrack insects' oleophilic cuticles, which allow them to resist wetting, are ineffective against oil. Logically, the predictability and susceptibility of indigenous wrack fauna make them good subjects for monitoring pollution.

Conclusion

This paper has shown the beach wrack community structure at Hazard Canyon Beach can be defined by three distinct stages of macroinvertebrate succession. The pattern is predictable for both types and numbers of species expected to be encountered in sand or wrack sampling positions during a given successional phase, but only quantitatively within the same cohort (i.e., islands deposited at the same time, same tidal height, and in close proximity). A "climax" stage is not achieved, and never will be, in high beach wrack because of physical or biological parameters which, after four or five weeks, result in deterioration of the ephemeral wrack resource. Thus, wrack faunal succession is not typical of that occurring in most marine or terrestrial systems, as the ratio of primary production to biomass decreases with progressing wrack decay.

Beach wrack is undoubtedly an essential resource to the sandy beach fauna, virtually providing islands of plenty in a sea of sand. To thoroughly understand how the variable physical and biological factors influence beach wrack community structure and faunal succession will require more indepth investigations. Future beach wrack studies should focus on the role the macro and microfauna play in wrack decomposition and succession both on the high beach and in the lower intertidal. Behavioral studies in the laboratory and the field combined with ex-

tensive physical data are essential. Perhaps with such information the ecological impact of parasitic forms and environmental pollutants as well as the interrelated effects of each species in the dynamic beach ecosystem could be determined.

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The Occurrence and Distribution of Terrestrial Isopods (Oniscoidea) on Santa Cruz Island with Preliminary Data for the Other California Islands

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Abstract.—The occurrence and distribution of terrestrial isopods (Oniscoidea) on Santa Cruz Island with preliminary data for the other California islands by R. Garthwaite, F. G. Hochberg, and C. Sassaman. *Bull. Southern California Acad. Sci.*, 84(1):23–37, 1985. During September and October of 1982 sixty locations on Santa Cruz Island, California, were examined for the presence of terrestrial isopods. Isopods were found at 58 of these locations. Thirteen terrestrial isopod species were found—seven littoral species and six non-littoral species. Eight of these species are Pacific coast endemics, three others are European introductions, and two are of uncertain origin. Terrestrial isopods on the island were found to be nearly as diverse as those on the adjacent mainland both with respect to the total number of species and the average number of species per collection site. The local distributions of littoral species on the island reflect the distributions of their preferred microhabitats. Microhabitat may also affect the distribution of non-littoral species, although there may be a significant historical component to their current distributions. Preliminary collection data are given for the other southern California islands.

While the terrestrial isopod (Oniscoidea) fauna of North America is depauperate when compared to many other areas of the world, it nevertheless forms a rather large and diverse assemblage. Although many aspects of terrestrial isopod taxonomy are still in turmoil, there are approximately 100 species north of Mexico, about one third being endemic (Van Name 1936). Many of the remaining species, indeed almost all of the widely distributed and commonly encountered ones, have been introduced into North America from the Old World (particularly Europe) by man (Van Name 1936).

Although terrestrial isopods are common and widely distributed throughout much of North America, precise distributional data are, more often than not, sparse and dated. This lack of records is certainly true of California. Even though the California fauna includes approximately 27 terrestrial isopod species, no comprehensive distributional studies have been reported. Those reports that do exist (Menzies 1950; Miller 1938, 1975; Richardson 1905; Van Name 1936; and others) are patchy and California oniscoids often have more extensive ranges than the literature indicates. Over the past several years we have been collecting isopods throughout North America and particularly in California. This paper reports the findings of a series of collections of terrestrial isopods made on Santa Cruz Island, California.

The biota of Santa Cruz Island has been the subject of extensive investigations (Philbrick 1967; Power 1980; for a review see Woodhouse 1981). Some of these investigations have been concerned with intertidal or littoral species and at least

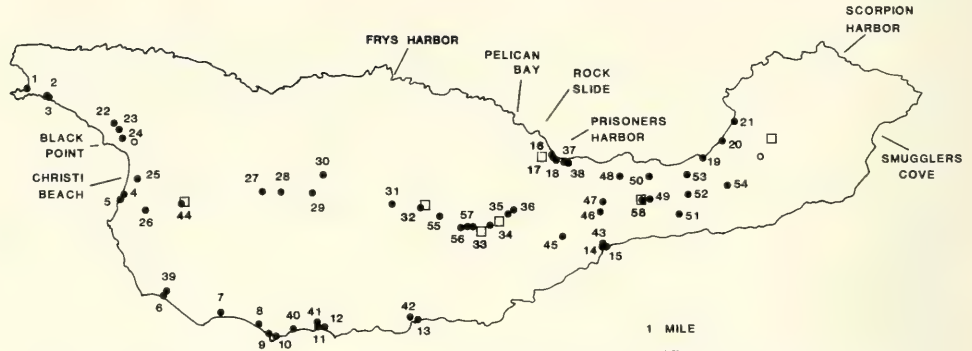


Fig. 1. Location of the 60 Santa Cruz Island sites examined in this study (see methods for criteria used in choosing collection sites). Closed circles represent sites where isopods were found. Open circles represent sites where apparently suitable habitat was examined but no isopods were found. Also indicated are locations from which oniscoids have been previously reported (see text), and the locations of the seven sites from which the Santa Barbara Museum of Natural History specimens were collected (squares).

three (Hewatt 1946; McGill 1978; Straughan and Hadley 1980) have reported the occurrence of oniscoids. There have been, however, no comprehensive reports on the terrestrial isopods of this island.

We examined a total of 60 sites on the island for terrestrial isopods during September and October of 1982. Sites were chosen by seeking out areas of suitable isopod habitat (i.e. more or less permanently damp places). If isopods were found in these habitats, representative samples were collected by hand (from a total area usually less than 2 sq m), returned to the laboratory alive, and identified using the following references: Hatch 1947; Menzies 1950; Miller 1975; Mulaik and Mulaik 1942; Richardson 1905; Schultz 1970; and Van Name 1936, 1940. Distribution records were supplemented by an additional seven collections (made in late March and early April of 1983) from the invertebrate collection at the Santa Barbara Museum of Natural History (see Fig. 1). The eastern end of the island and much of the northern coast were not examined by us because they are not easily accessible. Some of the other areas of the island (particularly the southwestern interior, Fig. 1) were surveyed for suitable habitats but contained none. Representative specimens are archived in the Department of Invertebrate Zoology at the Santa Barbara Museum of Natural History.

Results

Terrestrial isopods were quite common and widespread on Santa Cruz Island; we found isopods in all but two of the sites examined. Figure 1 shows the location of the 58 collection sites (closed circles) plus the two sites (open circles) where apparently suitable habitat was examined but no isopods were found. Also shown in Figure 1 are the locations of sites from which terrestrial isopods have been previously reported (see below).

Our collection sites can be divided into four categories with respect to habitat: 1) littoral sites (sites 1–21), 2) sites along permanent streams (sites 22–43), 3) sites near cattle troughs (sites 44–54), and 4) damp areas not associated with standing

water (sites 55–58). Thirteen species of isopods were collected on the island—seven littoral species: *Ligia occidentalis* Dana 1853, *Armadilloniscus holmesi* Arcangeli 1933, *Armadilloniscus lindahli* (Richardson 1905), *Littorophiloscia richardsonae* (Holmes and Gay 1909), *Alloniscus perconvexus* Dana 1856, *Alloniscus mirabilis* (Stuxberg 1875) (= *Alloniscus cornutus* Budde-Lund 1885; Schultz, pers. comm.), and *Tylos punctatus* Holmes and Gay 1909; and six non-littoral species: *Porcellio laevis* Latreille 1804, *Porcellio dilatatus* Brandt and Ratzeburg 1833, *Porcellio scaber* Latreille 1804, *Porcellionides* sp., *Armadillidium vulgare* (Latreille 1804), and *Venezillo microphthalmus* (Arcangeli 1932). Eight of the species collected are Pacific coast endemics (all of the littoral species plus *V. microphthalmus*), three are almost certainly European introductions (*P. laevis*, *P. dilatatus*, and *A. vulgare*), and two are of uncertain origin (*P. scaber* and *Porcellionides* sp.). Table 1 summarizes the occurrences of the thirteen species. A brief discussion of each species follows.

Pacific Coast Endemic Species

Tylos punctatus Holmes and Gay 1909

Tylos punctatus has a more southerly distribution on the mainland. It is common in Baja California, Mexico (Brusca 1980; Hamner, Smith, and Mulford 1968, 1969; Hayes 1977) and can be found sporadically in the San Diego area. North of San Diego it is much rarer and is seldom found north of Newport Bay (Garthwaite, unpublished data; Hayes 1977). *Tylos punctatus* is restricted entirely to sandy beaches where it burrows just above the most recent high tide line. On Santa Cruz Island this isopod is found on the west and southwest coasts (Table 1) where most of the extensive sandy beaches are located. A few individuals were collected at West End (site 3), Johnsons Lee (site 8), and the beach at Laguna Harbor (site 12). This isopod is exceedingly common, however, on Christi Beach (site 4) where it reaches densities similar to those found in Baja California. *Tylos punctatus* was also reported from Christi Beach (Fig. 1) by Hewatt (1946) and from Black Point (Fig. 1) by Straughan and Hadley (1980).

Ligia occidentalis Dana 1853

Ligia occidentalis is quite common on the mainland from San Francisco to the Gulf of California, Mexico (Garthwaite, unpublished data; Mulaik 1960; Van Name 1936), and was also common and widespread on Santa Cruz Island (Table 1), usually occurring on the more rocky beaches. Hewatt (1946) reported this species from Scorpion Harbor, Smugglers Cove, and the Prisoners-Pelican rock slide (Fig. 1). McGill (1978) collected *L. occidentalis* at Prisoners Harbor and Frys Harbor (Fig. 1).

Armadilloniscus holmesi Arcangeli 1933

This isopod is common on the southern California mainland and can be found from Washington to Magdalena Bay, Baja California, Mexico (Hatch 1947; Menzies 1950; Mulaik 1960; Schultz 1971). On the island it was found only at Christi Beach (site 5) and Chinese Harbor (site 19), however it did occur in considerable numbers at the latter site.

Table 1. Continued.

	Collection site																												
	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Pacific Coast endemics																													
<i>Tylos punctatus</i>																													
<i>Ligia occidentalis</i>																													
<i>Armadilloniscus holmesi</i>																													
<i>Armadilloniscus lindahli</i>																													
<i>Liitorophiloscia richardsonae</i>																													
<i>Alloniscus perconvexus</i>																													
<i>Alloniscus mirabilis</i>																													
<i>Venezillo microphthalmus</i>																													
European introductions																													
<i>Porcellio laevis</i>	100	100	10	9	58		1			100	11	100	98	50	59	2	8	84	98	100	100	28	100		60	25	6	100	
<i>Porcellio dilatatus</i>				1	3	52									10				1		33							6	
<i>Armadillidium vulgare</i>			33	90	37	100	11	1	94				50	41	88	84	16	1			33			40	25	86			
Uncertain origin																													
<i>Porcellio scaber</i>			57		2	36	99	6																			50	2	
<i>Porcellionides</i> sp.											3					8						6	100	100					

Armadilloniscus lindahli (Richardson 1905)

On the mainland, *A. lindahli* extends from Cedros Island, Baja California, Mexico, to the San Francisco area (Menziés 1950; Schultz 1971). On Santa Cruz Island only a few individuals were found at Chinese Harbor (site 19, Table 1).

Littorophiloscia richardsonae (Holmes and Gay 1909)

Littorophiloscia richardsonae is common and widespread on the mainland occurring at least from Cedros Island, Baja California, Mexico, to Washington (Garthwaite, unpublished data; Hatch 1947; Mulaik 1960; Van Name 1936). It was found in moderate abundance at several island localities (Table 1): Christi Beach (site 5), Willows Anchorage (site 13), Valley Anchorage (site 14), and Chinese Harbor (site 21). Although *L. richardsonae* usually has a gray-brown color, among the isopods collected at Willows Anchorage was a white individual which appeared to entirely lack pigmentation in both the eyes and body.

Alloniscus perconvexus Dana 1856

Alloniscus perconvexus is common and widely distributed along the mainland. It occurs at least from southern California to Washington (Garthwaite, unpublished data; Hatch 1947; Van Name 1936) but is much more common north of Point Conception than to the south (Garthwaite, unpublished data). *Alloniscus perconvexus* was widespread and common on Santa Cruz Island, and was collected at many of the littoral sites examined (Table 1). Like *T. punctatus* this species is restricted to sandy beaches and is thus found primarily on the west and southwest coasts of the island. This species also was reported from Scorpion Harbor and Christi Beach (Fig. 1) by Hewatt (1946), and specimens collected on Santa Cruz Island in 1939 are contained in the collections of the Los Angeles County Museum of Natural History (labeled Channel Islands biological survey). Both island and mainland populations of *A. perconvexus* are highly variable in color and usually closely match the color of the sand in which they live (Garthwaite, unpublished data). On the island, however, a few orange individuals were found (at Johnsons Lee, site 7; and the beach at Laguna Harbor, site 12) which closely approximated the color of the partially dried kelp fronds under which the isopods were burrowed.

Alloniscus mirabilis (Stuxberg 1875)

Alloniscus mirabilis has previously been collected at Laguna Beach (Stafford 1913) and San Diego Bay (USNM catalog #46093). On the mainland we have collected this species at Newport Bay (Orange Co.), Pebble Beach (San Mateo Co.), and Point Piedras Blancas (San Luis Obispo Co.). On the island it was collected at several littoral sites and one stream site close to the beach (Table 1).

Venezillo microphthalmus (Arcangeli 1932)

The range of *V. microphthalmus* is more northern on the mainland and it is not commonly encountered. It has previously been collected at two localities in Tulare County (Woodlake and Hammond; Mulaik and Mulaik 1942); Jackson, near Sacramento (Mulaik and Mulaik 1942); and Saratoga, near San Jose (Van Name 1936). On Santa Cruz Island two individuals were collected along the stream that drains into Willows Anchorage (site 42, Table 1), and several individuals

were encountered in Santa Barbara Museum specimens collected just west of Prisoners Harbor (Fig. 1).

European Introductions

Porcellio laevis Latreille 1804, *Porcellio dilatatus* Brandt and Ratzeburg 1833, and *Armadillidium vulgare* (Latreille 1804)

These three species are thought to have been introduced into North America by the actions of man (Van Name 1936). All three are common throughout California (Garthwaite, unpublished data; Miller 1938, 1975) and all three are also common on Santa Cruz Island (Table 1). *Porcellio laevis* and *A. vulgare*, in fact, are by far the most common non-littoral species on the island and together inhabit nearly all areas of suitable habitat examined (Table 1, Fig. 2). *Porcellio dilatatus* has a more restricted range on the island being found primarily in the east-central portion (Table 1, Fig. 2). Specimens of *P. dilatatus* collected on Santa Cruz Island in 1939 are contained in the collections of the Los Angeles County Museum of Natural History (labeled Channel Islands biological survey). Mainland populations of *P. laevis* often contain individuals which, instead of being the usual brownish-gray color with black eyes, are white with black eyes (Garthwaite, unpublished data). This color morph was also present on the island (site 33). Also present on the island (site 45) was a color morph of *P. dilatatus* which was visually indistinguishable from the tan morph described by Sassaman and Garthwaite (1980). This morph is rare but widespread in California (Sassaman and Garthwaite 1980). Finally, a white individual of *A. vulgare* was found at site 32 (base of La Cascada) which lacked eye and body pigmentation. Populations of *A. vulgare* typically show a great deal of color variation but individuals are usually some combination of gray, brown, and/or yellow.

Uncertain Origin

Porcellio scaber Latreille 1804

While this species is native to Europe and is thought by many to have been introduced to North America from Europe, there may also be a subspecies which is native to the Pacific Coast of North America (Arcangeli 1932; Hatch 1947; Miller 1938, 1975). *Porcellio scaber* is common all along the coast of California but has a more patchy distribution in inland areas of southern California (Garthwaite, unpublished data). It is moderately abundant on Santa Cruz Island, although it appears to be restricted primarily to the east-central portion of the island and Prisoners Harbor (Table 1, Fig. 2). Although *P. scaber* is usually dark gray in color, an orange individual with orange eyes was found at Prisoners Harbor (site 38). This color morph is similar in many respects to the tan morph of *P. dilatatus* (Sassaman, unpublished data) and, like the tan morph, is rare but widespread on the mainland (Sassaman and Garthwaite, unpublished data).

Porcellionides sp.

The *Porcellionides* on Santa Cruz Island is morphologically similar to *P. pruinosus* (Brandt). It has been assumed that *P. pruinosus* was introduced to North America by man and has subsequently spread across much of the continent (Van Name 1936). In the course of investigations on this species throughout North

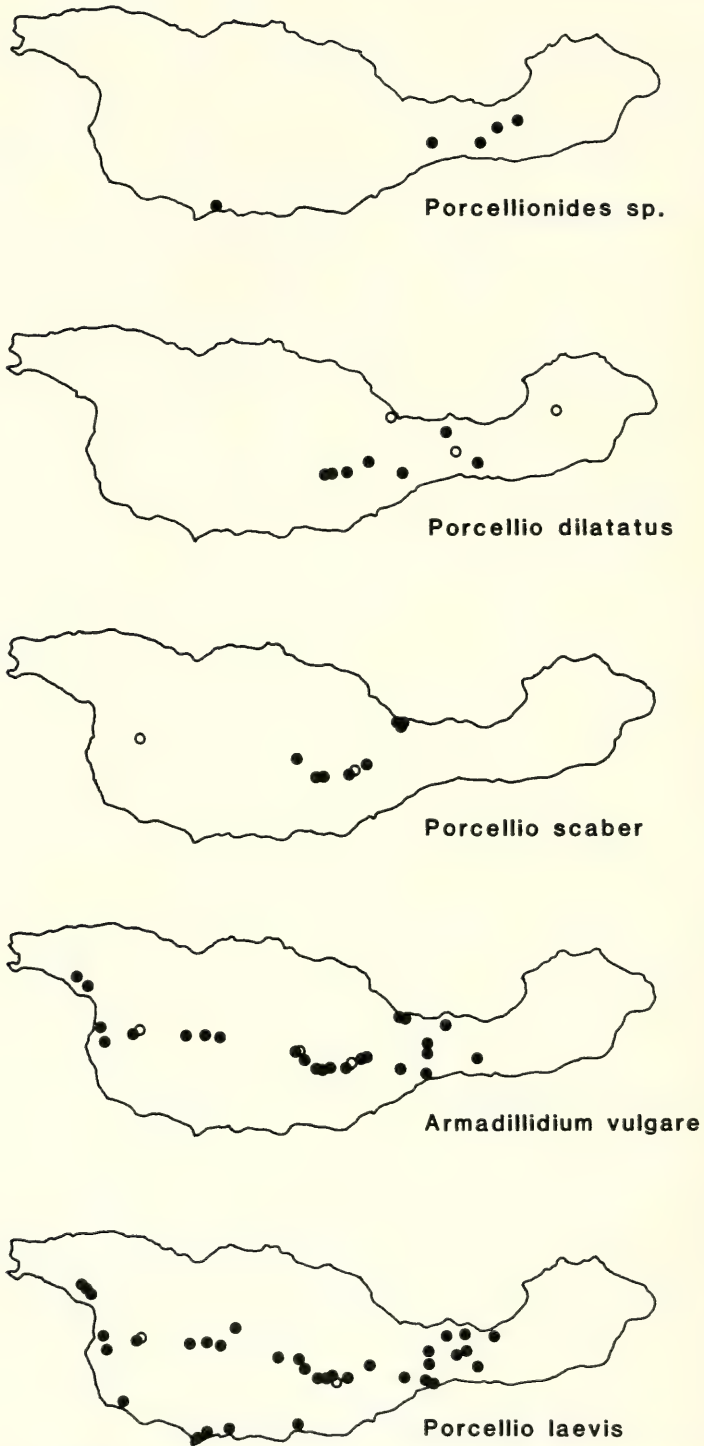


Fig. 2. The distributions of synanthropic species of terrestrial isopods on Santa Cruz Island. Closed circles represent collections made during this survey, open circles represent museum collections.

America, however, we have found that "*P. pruinus*" is not a homogeneous species (Garthwaite and Sassaman, in prep.). At least two forms exist which are genetically, reproductively, and geographically isolated from each other. The island specimens are similar to the southwestern individuals on the mainland. It is not clear at this point which of these species has been introduced from Europe and thus which of these species is truly *P. pruinus*. At any rate, *Porcellionides* sp. is widespread and common throughout mainland California (Garthwaite, unpublished data) and is fairly abundant on Santa Cruz Island as well (Table 1). On the island it appears to be restricted, for the most part, to cattle trough sites on the eastern portion of the island (Fig. 2).

Discussion

Perhaps the two most interesting aspects of the Oniscoidea of Santa Cruz Island are: 1) that when compared to the adjacent mainland the oniscoid fauna is not terribly depauperate, and 2) that they are so ubiquitous.

Table 2 contrasts the isopod species found on Santa Cruz Island with those found on the southern California mainland.* Santa Cruz Island possesses 13 species of terrestrial isopods and the southern Californian mainland 17. This diversity on the island is interesting in light of the fact that island faunas of terrestrial organisms are almost invariably depauperate when compared to mainland faunas. The California islands are not, in general, an exception (Power 1980).

It is not surprising that the oniscoids do not follow this trend. The terrestrial isopods of southern California can, for the most part, be divided into two categories: 1) littoral species (all of the endemic species listed in Table 2 except *Ligidium lapetum* Mulaik 1942, *Ligidium latum* Jackson 1923, *Protrichoniscus heroldi* Arcangeli 1932, and *Venezillo microphthalmus*) and 2) synanthropic species (the species listed under "European introductions" and "uncertain origin" in Table 2). Littoral species of oniscoids, because they live along the shore, are often washed by waves during high tides and storms and many are undoubtedly washed out to sea either individually or clinging to debris (Hayes 1977; Menzies 1952). Many (if not all) littoral oniscoids can survive for long periods of time in sea water (Brusca 1966; Hayes 1977; Parry 1953; Wilson 1970). These factors make littoral oniscoids excellent candidates for colonizers of off-shore islands.

Synanthropic species ought also to be good colonizers in areas of extensive human activity. Santa Cruz Island has a long history of human occupation (Glasgow 1980), and has, in past years and to a more limited extent today, been host to extensive ranching operations (Brumbaugh 1980).

Conspicuous by its presence on Santa Cruz Island is *Venezillo microphthalmus*, which has previously been reported only from central and northern California. Conspicuous by its absence from the island is *Mauritaniscus littorinus* (Miller 1936), which is a common and widespread littoral species on the adjacent mainland (Schultz, Garthwaite, and Sassaman 1982) and has also been found on San Miguel Island (see below). It is not surprising that neither *Ligidium lapetum*, *L.*

* Not included in the table is a species of *Venezillo* (probably *V. arizonicus* (Mulaik 1942)) which is common in the deserts of southern California (Garthwaite, unpublished data) but which, due to its burrowing habits, would not have been collected using our methods even if it occurred on Santa Cruz Island.

Table 2. Terrestrial isopods of the southern California mainland and islands. Not included is *Venezillo arizonicus*? (see text for details). 1) this paper, 2) Cockerell 1940, 3) Given and Lees 1967, 4) Hewatt 1946, 5) Hochberg 1981 (revised), 6) McGill 1978, 7) Straughan & Hadley 1980, 8) Sumner and Bond 1939, 9) Van Name 1940, 10) Santa Barbara Museum of Natural History, 11) Los Angeles County Museum of Natural History, 12) University of California Insect Survey, 13) see text for references.

	Southern California mainland	Island										
		San Miguel	Santa Rosa	Santa Cruz	West Anacapa	Middle Anacapa	East Anacapa	Santa Barbara	San Nicholas	Santa Catalina	San Clemente	
Pacific Coast endemics												
<i>Tylos punctatus</i>	13			1, 4, 7					7	7	11	
<i>Ligia occidentalis</i>	13	5, 6		1, 4, 6	5				6	3, 11		6
<i>Ligidium lapetum</i>	1											
<i>Ligidium latum</i>	1											
<i>Protrichoniscus heroldi</i>	12											
<i>Armadilloniscus coronacapitalis</i>		5			5							
<i>Armadilloniscus holmesi</i>	13			1								
<i>Armadilloniscus lindahli</i>	13			1								
<i>Littorophiloscia richardsonae</i>	13	5		1	5							5
<i>Alloniscus perconvexus</i>	13	5	5	1, 4, 11	5			2, 7, 9, 11		7		11
<i>Alloniscus mirabilis</i>	13	5		1	5			2, 9, 11				
<i>Mauritaniscus littorinus</i>	13	5										
<i>Venezillo microphthalmus</i>				1, 10	5	5		5				
European introductions												
<i>Haplophthalmus danicus</i>	13											
<i>Porcellio laevis</i>	13	2, 5	5, 11	1, 10		5	5	5, 8	11	5		2, 5
<i>Porcellio dilatatus</i>	13	5		1, 11, 10						5		5
<i>Armadillidium vulgare</i>	13		5	1, 10			5			2, 5		
Uncertain origin												
<i>Porcellio scaber</i>	13		5	1, 10	5			5				
<i>Porcellionides</i> sp.	1			1				5			2, 5	

latum, *Protrichoniscus heroldi*, nor *Haplophthalmus danicus* Budde-Lund 1877 were found on Santa Cruz Island since all four species are apparently quite rare in southern California, and the *Ligidium* spp. and *P. heroldi* are neither synanthropic nor littoral. We have found *L. lapetum* and *L. latum* only at Refugio Creek (west of Santa Barbara) in southern California and *H. danicus* only at Marina del Rey (Schultz et al. 1982) and Riverside. In southern California *P. heroldi* has been collected only at Deep Canyon (3.5 miles south of Palm Desert) (University of California Insect Survey specimen #323027) and nine miles east of Joshua Tree (Insect Survey #297405).

Several synanthropic species have distributions on Santa Cruz Island which may suggest a rather recent introduction via human activity. Three of these species (*Porcellio dilatatus*, *P. scaber*, and *Porcellionides* sp.) are restricted to the east-central portion of the island (Fig. 2). The distributions of these species correspond well with the major areas of human activity on the island. Most traffic to Santa Cruz Island is through Prisoners Harbor to the Stanton Ranch, the University of California Field Station, or the naval installation, all of which are in this east-central area.

Porcellio laevis and *Armadillidium vulgare* are two synanthropic species which have much wider distributions on the island (Fig. 2). The difference in distribution between *P. dilatatus*, *P. scaber*, and *Porcellionides* sp. on the one hand, and *P. laevis* and *A. vulgare* on the other, may indicate that the latter species have been on the island much longer and have had more time to disperse, and/or that they are more capable of dispersal than the former species. Miller (1938) found that *A. vulgare* and *P. laevis* were more capable of withstanding stresses of high temperatures and desiccation than *P. dilatatus*, *P. scaber*, and *Porcellionides* sp. This greater tolerance would presumably make them more capable of dispersal. The fact that oniscoids collected on Santa Cruz Island in 1939 (Los Angeles County Museum of Natural History) contain only *P. dilatatus* and *A. perconvexus* would argue against a historical cause for the differences in distributions among these species.

Alternately, the differences in the distributions of these isopods on Santa Cruz Island may be caused by their different habitat requirements. Miller (1938) noted that each of these species occupied a characteristic habitat and related this habitat choice to differences in the physiologies of the isopods. Thus, the east-central portion of Santa Cruz Island may have physical, climatic, and/or biotic aspects which differ from the rest of the island; and *P. dilatatus*, *P. scaber*, and *Porcellionides* sp. may not be able to extend their range due to lack of suitable habitat.

On Santa Cruz Island terrestrial isopods as a whole occupy nearly all areas of suitable habitat, being found at 58 of the 60 sites that we investigated. While we present no quantitative data, it is our experience that this is in sharp contrast to the situation on the mainland where large areas of apparently suitable habitat are not occupied (Garthwaite, unpublished data). For littoral species this difference may be due, in part, to human disturbance of mainland sites. For both littoral and non-littoral species it may also be an example of the phenomenon of density compensation and/or niche expansion (MacArthur, Diamond, and Karr 1972). Since island faunas are generally depauperate, those species that do exist there are able to increase in density or occupy niches in addition to those they would

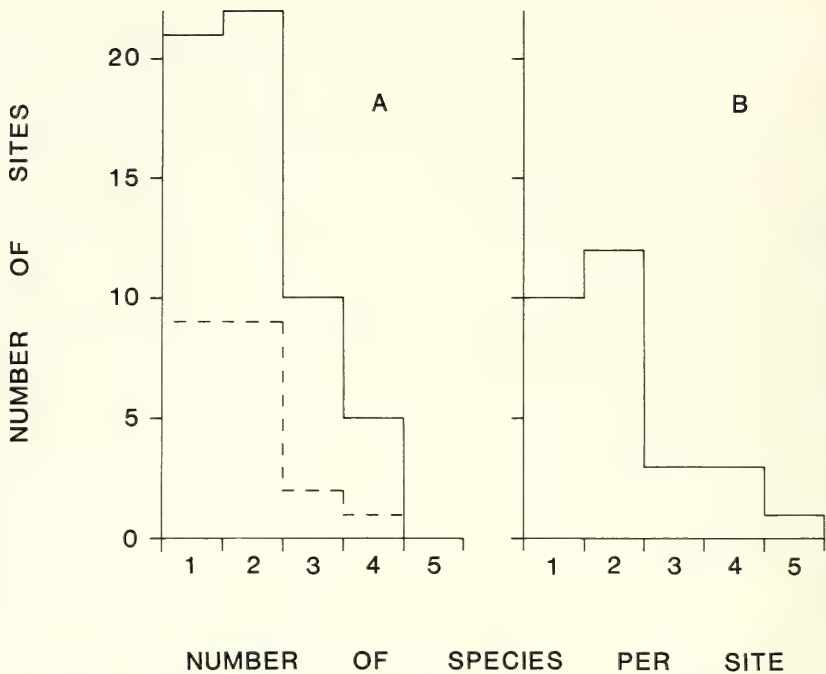


Fig. 3. The frequency distribution of species diversity among: A) 58 Santa Cruz Island sites (mean = 1.98), and B) 29 southern California mainland sites (mean = 2.07). Broken line = littoral sites, solid line = littoral and non-littoral sites.

occupy on the mainland because of the absence of competitors and/or predators. Thus oniscoids in general may be more common and widespread on Santa Cruz Island because competitors and predators are absent. A wide variety of animals apparently prey on oniscoids including birds (Schmidt & Olsen 1964), shrews, spiders, centipedes, frogs, carabid beetles (Sutton 1970, 1972), and opossums. Even though almost all mainland species of oniscoids occur on the island, some of these species have restricted ranges on the island as discussed above (Fig. 2). Thus isopods in some areas of Santa Cruz Island may be undergoing density compensation and niche expansion because competing species of oniscoids which have recently been introduced to the island have not yet dispersed to these areas. Density compensation and/or niche expansion have been found in several other organisms on the California islands including foxes (Laughrin 1980), birds (Diamond and Jones 1980), land snails (Hochberg, unpublished data), and plants (Philbrick 1980). *Traskorchestia traskiana* (Stimpson 1857), an amphipod which is very similar in ecology to many terrestrial isopods, also has been found to be more widespread on Santa Cruz Island than on the mainland (Busath 1980).

It is interesting to note that while oniscoid diversity on the island and mainland is rather high, the diversity at any one site is rather low. Figure 3 shows the frequency distribution of species diversities among the island sites along with data from comparable mainland sites. The mode of the island distribution is 2 species/site. Thus, while a total of 13 species of oniscoids was found on Santa Cruz Island,

most sites contained only a small number of these species (usually about 2). Mainland sites are similar to island sites in both the mode of species found per site and in the distribution of sites around this mode (Fig. 3).

The low number of species per site is easy to understand in light of Miller's work (1938), our own observations, and the observations of others (Edney 1968; Schultz 1972), which suggest that different species of oniscids have significantly different microhabitat requirements. The difference in habitat between littoral and non-littoral species is obvious, but even within the littoral species there is a wide variety of microhabitats. *Ligia occidentalis* is found on or under rocks on the more rocky beaches. *Tylos punctatus* and *Alloniscus perconvexus* are found only on sandy beaches where they burrow into the sand at approximately the high tide line. *Armadilloniscus holmesi* and *A. lindahli* usually occur on rocks under freshly beached kelp. *Littorophiloscia richardsonae* inhabits similar rocky shores but is found higher up under drier kelp and other debris. Finally, *Alloniscus mirabilis* is usually found under rocks well above the high tide line. Non-littoral oniscids may similarly subdivide the habitat on physiological grounds (Miller 1938).

Less extensive collections have been made by one of us (FGH; see Hochberg 1981) on the other southern California islands. These data (with minor modifications), along with records obtained from the collections of the Los Angeles Museum of Natural History, the Santa Barbara Museum of Natural History, and previous reports from the literature, are summarized in Table 2. While the faunal list for other islands is preliminary, since it does not represent the same degree of collecting effort that the Santa Cruz Island data do, it nevertheless demonstrates several important points. First, terrestrial isopods are, in general, widespread and common on the islands. Second, two species in addition to the 13 found on Santa Cruz Island occur on other islands: *Mauritaniscus littorinus*, the only southern California littoral species not found on Santa Cruz Island, was collected on an adjacent island (San Miguel); and *Armadilloniscus coronacapitalis* Menzies 1950, a species previously reported only from Tomales Bay (north of San Francisco), was collected on San Miguel and Anacapa Islands. Third, *Venezillo microphthalmus*, which was previously reported only from central California, appears to be rather widespread on the islands, occurring on Anacapa and Santa Barbara Islands in addition to Santa Cruz Island.

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A New Species of *Pseudeurythoe* (Polychaeta: Amphinomidae) from Central California

Jerry D. Kudenov and James A. Blake

Abstract.—A new species of *Pseudeurythoe* (Polychaeta: Amphinomidae) from central California by Jerry D. Kudenov and James A. Blake. *Bull. Southern California Acad. Sci.*, 84(1):38–40, 1985. A new intertidal amphinomid polychaete of the genus *Pseudeurythoe* is described from the Elkhorn Slough in central California. The species is compared to related congeners.

The genus *Pseudeurythoe* Fauvel (Polychaeta: Amphinomidae) is represented by 13 described species (Fauchald 1972; Kudenov 1975), four of which occur in the eastern Pacific. During the course of a benthic survey of the Elkhorn Slough, one of us (JAB) discovered a single specimen of an as yet undescribed species of *Pseudeurythoe*. That species is described here and compared with related congeners. The holotype is deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Pseudeurythoe Fauvel
Pseudeurythoe reducta, n. sp.
Figure 1

Material examined.—CALIFORNIA: Moss Landing, Elkhorn Slough, June, 1976, Sta. 51A, 100 m north of thermal outfall, high intertidal zone, in fine sand. J. A. Blake collector—(Holotype, USNM 97288).

Description.—Holotype complete but fragmented, measuring 50 mm long and 6 mm wide for 96 setigers. Body elongate, widest anteriorly, tapering posteriorly, nearly rectangular in cross section; color in alcohol pink due to prior staining by Rose Bengal.

Prostomium pear-shaped, longer than wide (Fig. 1a); anterior lobe with smooth anterior margin, a pair of posteriorly located digitiform antennae and two ventrolateral cirriform palps; posterior lobe one-half as long as anterior lobe, bearing two pairs of well developed eyes, a small posteriorly located digitiform median antenna, and a short, pad-shaped caruncle on setiger 1, obscured by segmental folds of setigers 1–3.

Parapodia biramous throughout, with those of setiger 1 greatly reduced, inconspicuous (Fig. 1a). Typical parapodia with widely separated rami (Fig. 1b). Notopodia reduced to papillar lobes; neuropodia well developed, projecting beyond body wall (Fig. 1b). Dorsal and ventral cirri cirriform throughout, tapering, pointed, with those of setigers 1–4 appearing about equally developed (right ventral cirrus of setiger 2 missing from holotype) (Fig. 1a); ceratophores smooth.

Branchiae from setiger 2 continuing to the end of the body; branchiae arising as tufts resembling dendritic processes on posterior notopodial surfaces (Figs. 1a–b).

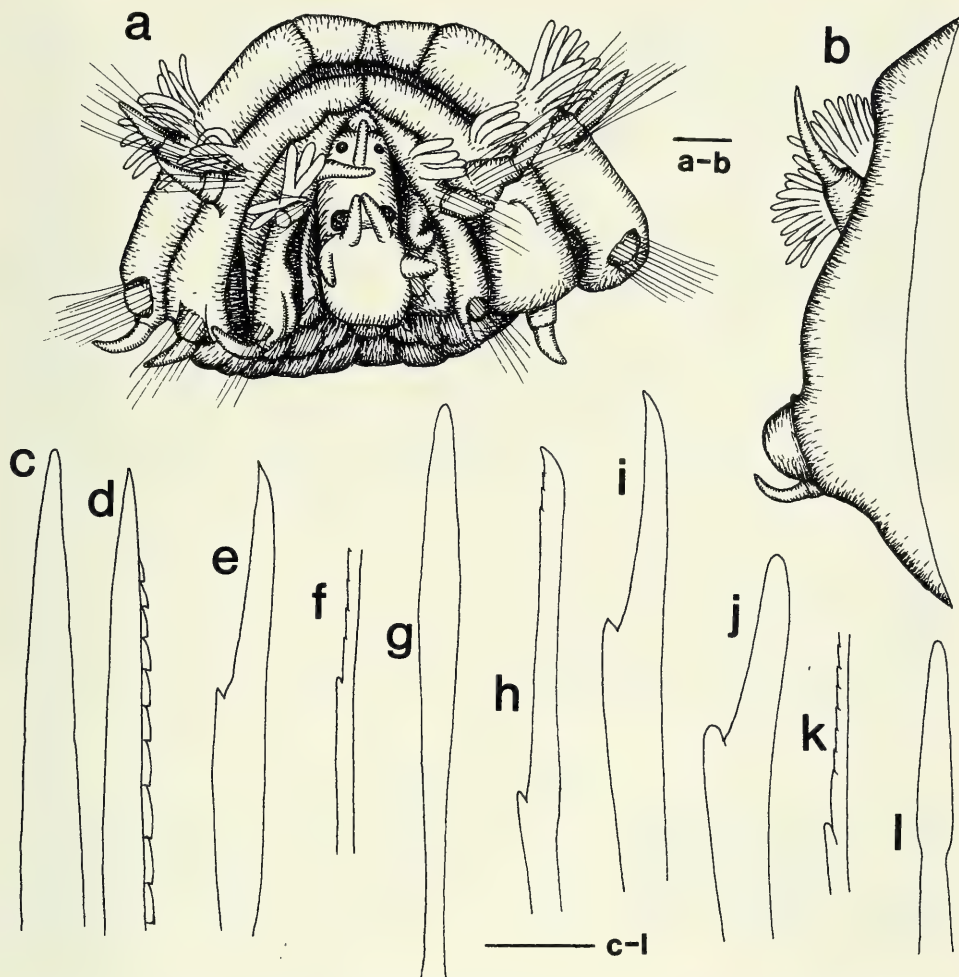


Fig. 1. a-l. Holotype, USNM 97288, *Pseudeurythoe reducta*. a, anterior segments, frontal view; b, median parapodium, anterior view; c, thick, smooth notosetal spine; d, harpoon notoseta, lateral view; e, forked notoseta, lateral view; f, serrated capillary seta showing detail of spur, lateral view; g, notoaciculum, lateral view; h, thin-shafted, forked neuroseta, lateral view; i-j, thick-shafted, forked neuroseta, lateral view; k, serrated capillary neuroseta showing detail of basal spur, lateral view; l, neuroaciculum, lateral view. Scales: a-b = 0.2 mm; c-l = μm .

Notosetae of six kinds; 1) thick, smooth spines (Fig. 1c); 2) harpoon setae (Fig. 1d); 3) forked spines with denticulate cutting margins (Fig. 1e); 4) long, slender smooth capillaries; 5) long, slender, basally spurred capillaries with denticulate cutting margins (Fig. 1f); and 6) long, distally inflated acicula numbering four per notopodium (Fig. 1g). Neurosetae of four kinds: 1) forked spines having thin shafts and long, distally serrated cutting margins (Fig. 1h); 2) forked spines having thick shafts and smooth cutting surfaces (Figs. 1i-j); 3) slender, conspicuously spurred capillaries having denticulate cutting margins (Fig. 1k); and 4) stout, distally inflated acicula, numbering three per neuropodium (Fig. 1l).

Pygidium dorsal with a midventral terminal papilla.

Remarks.—*Pseudeurythoe reducta* belongs to a small eastern Pacific species group in which the branchiae extend the full length of the body instead of being limited to anterior segments as is typical for the genus. Related species include *P. oculata* (Treadwell) and *P. tripunctata* Kudenov. *P. reducta* differs from both of these species in that branchiae are first present from setiger 2 instead of 3. As a group, all three species occur intertidally and are related ecologically and zoogeographically as well as morphologically. *P. reducta* is the most northern species, occurring in sand-mud sediments of central California. *P. tripunctata* and *P. oculata* occur either in mangroves or sandy sediments of western Mexico and Central America (Treadwell 1941; Kudenov 1975; Fauchald 1977).

Very little is known concerning the habits and mode of life of *Pseudeurythoe* species. Despite an older census (MacGinitie 1935) and numerous recent studies by the Moss Landing Marine Laboratories only a single complete specimen of *P. reducta* has turned up in the Elkhorn Slough, now a National Marine Sanctuary. It is possible that the habits of *P. reducta* are cryptic. A species tentatively identified as *P. ambigua* Monro has been reported from box core samples in the lower Chesapeake Bay (Karl, Diaz, Boesch, and Kravitz 1980). This species has been shown to be most abundant in anoxic sediments below 10 cm and is greatly undersampled by grabs. It is possible that *P. reducta* occupies a similar deep habitat in sediments of California estuaries.

Etymology.—The epithet, *reducta*, refers to the remarkable reduction of setiger 1. It is regarded as a noun in apposition.

Distribution.—Elkhorn Slough, California.

Acknowledgments

We are grateful to Nancy Maciolek Blake for reading and commenting on this paper. Rod Bertelsen supplied ecological information on the Chesapeake Bay species. The specimen on which this report is based was collected as part of a 316A demonstration survey of the Elkhorn Slough for Pacific Gas & Electric Company.

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Optimal Foraging in Barn Owls? Rodent Frequencies in Diet and Fauna

Orlando A. Schwartz¹ and Vernon C. Bleich²

Abstract.—Optimal foraging in Barn Owls? Rodent frequencies in diet and fauna by Orlando A. Schwartz and Vernon C. Bleich. *Bull. Southern California Acad. Sci.*, 84(1):41–45, 1985. We determined the frequencies of prey in the diet of Barn Owls by identifying mammal crania contained in pellets, and we determined the frequencies of prey items in the fauna by live and snap trapping. Data from two sites in Southern California showed approximately equal portions of prey in the diet and in the fauna. Such agreement may be expected when the predator perceives a low quality habitat, or it might be due to efficient predation methods that eliminate some of the constraints that face foraging predators.

The theory of optimal foraging, summarized by Pyke et al. (1977) and Krebs (1978), was developed as a predictive ecological and evolutionary algorithm. Models of this theory attempt to predict an animal's food choices including optimal particle size in the diet, the choice of which patch to feed in, when to switch patches, and the pattern of speed and movement within and between patches. Such optimal choices by an animal are contingent on and perhaps constrained by a species' ability to perceptually gather and neurologically process and store information regarding its past foraging activities and the future potential location of prey items. Ants were shown to make efficient choices of foraging patches and particle size (Taylor 1977; Davidson 1977), and backswimmers were shown to be able to assess prey density and thus decide what proportion of a prey to consume (Sih 1980). Therefore, animals as perceptually and neurologically simple as insects make near optimal diet choices.

The perceptual and predatory abilities of owls are well known. As first reported in the classic work by Dice (1945), owls were successful in obtaining prey in extremely low light and in darkness using only sound to locate prey. The prey of owls is perhaps as well known as that of any other animal group. They ingest prey items whole and then regurgitate undigestible and largely intact skeletal remains which are readily identifiable. There have been few studies attempting to assess owl prey choice relative to prey density and dispersion (Jaksic and Yanez 1979) or prey size (Marti and Hogue 1979).

In this paper we report the frequency of food items in the diet of Barn Owls (*Tyto alba*) and the corresponding frequencies of food items in this species' habitat at two Southern California study sites. With these data we have suggested qualitatively that a forager with evolutionarily advanced perceptual capacities may have much greater latitude in foraging than predicted by present theory.

Materials and Methods

One study site was the U.S. Naval Weapons Station, Fallbrook Annex, located in northern San Diego County, California. We observed Barn Owls inhabiting

and nesting in abandoned, wooden water towers on the Annex. A sample of pellets containing 1541 skulls was collected in these towers in May 1974. Bleich (1973) reported abundances of small mammals from over 4000 trap-nights at the Annex, and his data are used here for comparisons with owl pellet data. In this area patches of different vegetation and mammals occur in close proximity to one another, and the location of patches depends on soil type, slope, moisture availability, and solar exposure on hillsides. North facing slopes are characterized by Chaparral communities (2.0 km² total area on the Annex); south facing slopes are characterized by Coastal Sage Scrub communities (10.5 km²); and Grassland (19.8 km²), Southern Oak Woodland (0.5 km²), and Streamside Woodland (0.5 km²) are found where conditions are suitable.

On the Annex the following species were found at their highest densities and were considered typical species in the following communities (Bleich 1973) (though most were caught in other communities at much reduced densities): Chaparral: *Neotoma fuscipes* and *Reithrodontomys megalotis*; Coastal Sage Scrub: *Dipodomys agilis* and *Neotoma lepida*; Grassland: *Dipodomys stephensi*; Southern Oak Woodland: *Peromyscus boylii*; Streamside Woodland: *Peromyscus californicus*, *Peromyscus eremicus*, and *Microtus californicus*. The Annex is nearly surrounded by urban areas and avocado orchards, so the owls were presumed to forage mostly on the Annex land.

Our second study site was in the Carrizo Plains, an area of grazed, Central Valley Grassland, 19 km north of Reyes Station, San Luis Obispo County, California. We collected pellets containing 997 skulls during March 1974 and January 1975. The pellets were found inside abandoned water tanks, and Barn Owls were seen in the tanks on both collecting trips. We conducted 1077 trap-nights of trapping during late October 1971, January 1973, and March 1974, approximately 1.0 km from the site of the owl roosts. Vegetation was nearly uniform throughout the Carrizo Plains and consisted of low grasses and forbs, and sparse stands of Mormon tea (*Ephedra* sp.) and saltbush (*Atriplex* sp.).

The upper cranial portion of all skulls was identified to genus and, where possible, to species. Average weights of mammalian species used in data analyses were obtained from the literature (Hawbecker 1945; Fitch 1947; Schwartz and Bleich 1975), and from specimens in the collections of California State University, Long Beach, and the Museum of Natural History, University of Kansas.

Results

Species and numbers of skulls from the Fallbrook pellets were as follows: Botta's pocket gopher, *Thomomys bottae* (549); California vole, *Microtus californicus* (303); agile kangaroo rat, *Dipodomys agilis* (199); woodrat, *Neotoma* spp. (150); Stephens' kangaroo rat, *Dipodomys stephensi* (137); pocket mouse, *Perognathus* spp. (102); deer mouse, *Peromyscus* spp. (89); birds (6); western harvest mouse, *Reithrodontomys megalotis* (4); desert shrew, *Notiosorex crawfordi* (1); and desert cottontail, *Sylvilagus audubonii* (1). Species and numbers of skulls from the Carrizo Plains pellets were as follows: San Joaquin pocket mouse, *Perognathus inornatus* (299); Heermann's kangaroo rat, *Dipodomys heermanni* (254); Fresno kangaroo rat, *Dipodomys nitratooides* (209); giant kangaroo rat, *Dipodomys ingens* (96); *Peromyscus* and grasshopper mouse, *Onychomys* spp. (75); *Neotoma* sp.

Table 1. Frequencies of numbers and biomass of species common to the fauna of the two study areas in California and diet of Barn Owls inhabiting the areas.

Species	Weight g	Propor- tion of numbers in diet	Propor- tion of numbers in fauna	Difference	Propor- tion of biomass in diet	Propor- tion of biomass in fauna	Difference
Fallbrook Weapons Annex							
<i>M. californicus</i>	50	30.8	0.4	+30.4	22.6	0.4	+22.2
<i>D. agilis</i>	40	20.2	13.9	+6.3	13.5	13.9	-0.4
<i>Neotoma</i> spp.	150	15.2	16.2	-1.0	38.0	44.2	-6.2
<i>D. stephensi</i>	60	13.9	18.2	-4.3	13.9	19.8	-5.9
<i>Perognathus</i> spp.	25	10.4	27.2	-16.8	4.3	12.4	-8.1
<i>Peromyscus</i> spp.	30	9.0	23.8	-14.8	4.5	13.0	-8.5
<i>R. megalotis</i>	25	0.4	0.3	+0.1	0.2	0.3	-0.1
Carrizo Plains							
<i>D. heermanni</i>	50	33.0	48.6	-15.6	37.0	45.7	-8.7
<i>D. nitratoides</i>	35	40.1	30.4	+9.7	21.3	20.0	+1.3
<i>D. ingens</i>	130	15.1	12.4	+2.7	36.3	30.3	+6.0
<i>Peromyscus</i> and <i>Onychomys</i> sp.	25	11.8	8.6	+3.2	5.4	4.0	+1.4

(30); *Thomomys bottae* (20); birds (10); *Reithrodontomys megalotis* (3); and bat (1).

Several prey items did not appear in our trap samples. The pocket gopher, *T. bottae*; desert shrew, *N. crawfordi*; desert cottontail, *S. audubonii*; and birds and bats are seldom if ever caught in the Sherman collapsible and snap traps we used. We caught no *Perognathus inornatus* or *Neotoma* in our Carrizo Plains trapping perhaps indicating that there were owl foraging areas we did not sample. The little pocket mouse, *Perognathus longimembris*, is almost identical to *P. inornatus* (Hall and Kelson 1959) and *P. longimembris* was shown to hibernate for up to 5 months during the cold season of the year (French 1976; Kenagy 1973). We trapped in the Carrizo Plains only during the months of October, January, and March, and if *P. inornatus* also hibernates, that could explain its absence from our sampling.

Trapping data and pellet data were compared in proportions of numbers and biomass for species contained in both trap and pellet collections from each area (Table 1). To attempt to better estimate prey density and biomass proportions of species in the fauna of the Fallbrook Annex, numbers of each species trapped were weighted by multiplying the proportions of species in trapping samples by the total area of the different vegetational communities occupied by that species. We considered the Carrizo Plains to be a homogeneous habitat, so proportions of species in the trapping data were considered to be equivalent to proportions of species in the fauna. Proportions of biomass in the fauna and diet were computed by multiplying the proportion of that species in the sample by the average weight of that species.

We declined to calculate a goodness of fit statistic between diet and fauna. It would show a significant difference, but only because of data from *M. californicus* and *D. heermanni*. Here we emphasize the remarkable degree of similarity in diet and fauna and consider a statistical analysis inappropriate.

Discussion

With two exceptions, one at each study site, the results show approximately equal proportions of numbers and biomass in the diet of owls and in the fauna. The exceptions are in the 50 g weight class, *D. heermanni* and *M. californicus*, which were underrepresented in the diet of the Carrizo Plains owls and overrepresented in the diet of the Fallbrook owls, respectively. The difference between diet and fauna relative to *D. heermanni* may be explained by an unusual susceptibility to trapping, ability to avoid owl predation, or deficiencies in our sampling methods. The difference in diet and fauna in *M. californicus* may be explained as follows. Bleich (1973) trapped this species only in meadows associated with streamside woodlands, but it is widely reported to occur in California Grassland communities (Lidicker 1978). Our trapping could have occurred during a low density phase of this cyclic rodent. According to optimal foraging theory owls should switch to a high intensity search in high density patches (Krebs 1978) should such an abundance of this meadow dwelling vole occur. Given that the 50 g weight class (relative to the fauna) was overrepresented in the owl's diet in one area and underrepresented in the other, obviously these biases are not due to particle size/weight. Rather these data suggest there is no optimal particle size through a broad range of rodent size classes.

For approximately equal proportions of species to occur in diet and fauna, owls must effectively utilize all patches where patchy habitat occurs and they must attempt and regularly succeed in capturing all species encountered. Agreement in proportions of items in diet and fauna may occur when the predator perceives relatively low quality foraging opportunities (Krebs 1978). We suggest in this owl that it may also be due to superior perceptual and predatory ability not requiring "complex strategies" to successfully meet nutritional requirements.

Our data and analyses were crude and our conclusion is only one possible explanation of these data. We had no opportunity to follow prey population dynamics that would change patch quality and perhaps owl foraging patterns. Similarly, we had no data to suggest optimal owl foraging strategies that could be superimposed on these data or have changed with changes in the communities thus allowing optimal habitat utilization while still achieving close similarity in frequencies of items in diet and fauna. Future research on owl foraging dynamics could provide interesting extensions of optimal foraging theory.

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Research Notes

Record of the Pacific Burrfish from Southern California

On 27 December 1982, the junior author received a telephone call from the Long Beach Marine Safety Division regarding an unusual fish. The specimen, 198.5 mm SL, 235.0 mm TL, and 456 g (after preservation), was found in relatively fresh condition washed ashore in Long Beach Harbor on Cherry Avenue Beach. It was identified by us as *Chilomycterus affinis* Günther, the Pacific burrfish. In Günther's (1870) original description of *C. affinis*, the taxon was based upon a "Stuffed [specimen], 15 inches long"; type-locality was unknown. In 1891, Eigenmann described *Chilomycterus californiensis* based on a single specimen from San Pedro, California. "On account of the unreasonable price asked for it I [Eigenmann] did not obtain it" However, two years later Eigenmann (1893) redescribed *C. californiensis* and stated: "During the summer of 1891 a fisherman captured a specimen of a *Chilomycterus* near San Pedro, Cal. He preserved it in alcohol and offered it for sale. The price asked was so unreasonably high that I merely took some notes of it. Since then it has been procured by the National Museum, and I am able to redescribe it. This is apparently the first notice of a *Chilomycterus* on the Pacific coast of North America." An illustration of the specimen (Plate LXXXI.) is included in Eigenmann's second paper. The type is No. 43860 in the U.S. National Museum. *Chilomycterus californiensis* has since been treated as a junior synonym of *C. affinis*. Both Snodgrass and Heller (1905) and Jordan and Evermann (1905), in their respective studies on Pacific fishes, considered these two nominal species as synonymous. We are aware of but three bonafide records of *C. affinis* from Californian waters.

Following Eigenmann's 1891 record of *Chilomycterus* from California, a second burrfish was not noted until June 1959, from Newport Beach (Radovich 1961). This specimen, 223 mm SL, is housed in the ichthyological collection, University of California, Los Angeles, W59-219 (Donald G. Buth, Univ. Calif. Los Angeles, pers. commun.). Regarding the Pacific burrfish, Fitch and Lavenberg (1975) state, "no more than three or four individuals have been seen or captured in our waters." Data on these additional specimens are sketchy at best, no dates or localities are available (Robert J. Lavenberg, Natural History Museum of Los Angeles County, pers. commun.). The first two Californian captures (1891 and 1959) were made during periods of unusually warm marine water. Late 1982 marked the beginning of a period of higher than normal ocean temperatures in the eastern Pacific and has been associated with the El Niño phenomenon. Temperature anomalies at the sea surface in one degree squares off southern California for October through December 1982 were up to 2.2°C above the long term mean (Douglas R. McLain, National Marine Fisheries Service, pers. commun.). It is significant that all three documented captures of *C. affinis* from southern California were taken during periods of warm water.

Biogeographically, *C. affinis* has a broad and somewhat unusual distribution—tropical and subtropical eastern Pacific including Galapagos Islands, the Hawaiian

Islands, and Japan; nowhere is *C. affinis* common. The systematics of the genus *Chilomycterus* are in need of review. The Long Beach specimen is deposited at the Natural History Museum of Los Angeles County, LACM 43449-1.

Acknowledgments

We would like to thank the Long Beach Safety Division, particularly lifeguard Kelly Coultrup for bringing the Pacific burrfish to our attention. The curators at the following institutions checked their respective collections for material of *C. affinis*: California Academy of Sciences, Natural History Museum of Los Angeles County, Scripps Institution of Oceanography, and University of California at Los Angeles. Douglas R. McLain provided temperature anomaly charts of the eastern Pacific Ocean.

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Electrophoretic Comparison of Two Southern California Chipmunks (*Tamias obscurus* and *Tamias merriami*)

The chipmunk *Tamias obscurus davisi* (Callahan) was given species status by Callahan (1977) based on bacular morphology. Except by the ossa genitalia, *Tamias obscurus* is not readily distinguished from *T. merriami merriami* J. A. Allen, which led to our interest in the systematics of these species. Sympatric in the San Bernardino Mountain range north of the San Gorgonio pass and in the San Jacinto Mountains of southern California, *Tamias merriami* extends north to the Sierra Nevada (see Hall 1981) whereas *T. obscurus* is found south as far in Baja California as San Pablo (Callahan 1977).

Esterases have been used in genetic studies of mice (Selander, Smith, Yang, Johnson, and Gentry 1971) and their value in assessing squirrel taxonomy was suggested by Seaman and Nash (1977). Esterases also have been used in the construction of taxonomic keys (Seaman 1975). Because they are easily acquired in the field by sampling peripheral blood, we chose to use these enzymes in evaluating the systematic relationships of *Tamias obscurus* and *T. merriami*.

Horizontal starch gel electrophoresis was performed using the blood hemolysate of a total of 24 individuals of *Tamias* from southern California and Washington.

1. *Tamias obscurus* (5 males, 5 females) Riverside County, 4 km on Black Mountain Road from highway 243, in the San Jacinto Mountains of California.
2. *Tamias obscurus* (2 males, 2 females) San Bernardino County, 5 km north of Onyx Pass on Highway 38, in the San Bernardino Mountains of California.
3. *Tamias merriami* (4 males, 3 females) Riverside County, 2 km on Black Mountain Road from Highway 243, in the San Jacinto Mountains of California.
4. *Tamias speciosus* (1 male, 1 female) San Bernardino County, 4 km east of Heart Bar State Park Campground, in the San Bernardino Mountains of California.
5. *Tamias amoenus* (1 female) from Kittitas County, 2 km north of Cliffdell, Washington.

The chipmunks were live trapped and taken to the laboratory where blood was acquired by toe-clipping, this way the same individual could be assayed again for verification of results. The specimens were eventually deposited in the Loma Linda University Museum of Natural History and genital bones preserved for species identification.

The preparation of the hemolysate, the electrophoretic procedure, and the staining technique were similar to Selander et al. (1971), with the exception that blood was collected in capillaries and frozen immediately to produce lysis before applying the samples to the gel. The samples were run at not more than 200 volts and about 35 ma for 6 hours. After electrophoresis the starch-gels were sectioned into four horizontal slices and stained separately as in Selander et al. (1971).

The hemolysate of *Tamias obscurus* and *T. merriami* was analyzed for 11

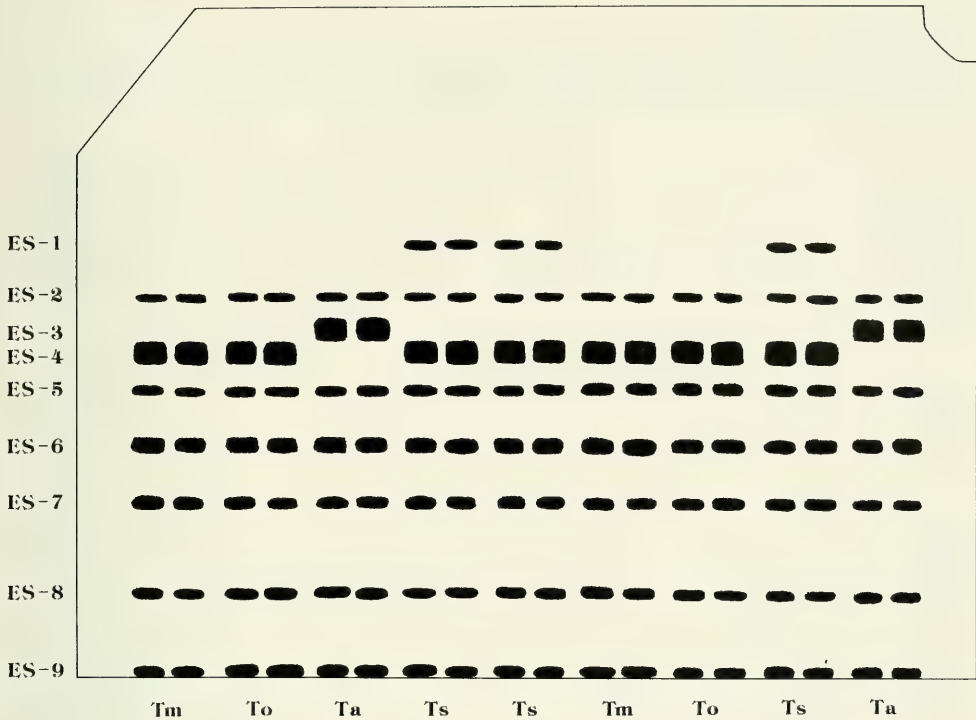


Fig. 1. Drawing of an actual gel used to compare the four species of chipmunks in this study. The samples are applied in replicate. Tm = *Tamias merriami*, To = *Tamias obscurus*, Ta = *Tamias amoenus*, Ts = *Tamias speciosus*, ES = Esterase.

different enzymes: malate dehydrogenase, glutamate oxalate transaminase, esterase, phosphoglucisomerase, acid phosphatase, glutamic acid dehydrogenase, phosphoglucumutase, fructose-6-phosphate dehydrogenase. Of the above all were either monomorphic or unscorable. Catalase, shikimic acid dehydrogenase and peroxidase were not present in the hemolysate of these species. Esterase was chosen for further study because it was found to be polymorphic in ground squirrels (unpublished data).

The esterases present in chipmunks consist of 7 bands (see Fig. 1), which correspond to those of mice (Petras and Biddle 1967). Of these seven bands, no consistent differences were found between *Tamias obscurus* and *T. merriami*. There was no sexual dimorphism detected in esterase, and populations in the San Jacinto Mountains were indistinguishable from those in the San Bernardino Mountains.

Since interspecific esterase polymorphism for *Tamias obscurus* and *T. merriami* was absent, two individuals of *T. speciosus* were used for comparison on the same gels. *Tamias speciosus* differs from *T. merriami* and *T. obscurus* by the presence of a fast band, ES-1. One individual of *Tamias amoenus* was also used for comparison and differed from *T. merriami* and *T. obscurus* in the relative mobility of ES-3, and from *T. speciosus* by the absence of ES-1.

The electrophoretic description of *Tamias obscurus* and *T. merriami* was rather puzzling when compared with the consistent polymorphism of squirrel and chip-

munk plasma proteins reported by Seaman and Nash (1977). They observed differences between the species they studied. The potential for polymorphism and the likelihood of unique proteins being present is suggested by the differences between the other two species of chipmunks in our study.

A difficulty with the systematics of chipmunks is the major emphasis which has been placed on bacular morphology. The baculum has been implicated in reproductive isolation by a "lock and key" mechanism (Patterson and Thaeler 1982) however. The genetic basis for bacular morphology has not been explained.

This is a preliminary study and further systematic work should be done to determine the nature of genetic variability in chipmunk species.

Acknowledgments

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Notes on Spawning in the Dolphin Fish, *Coryphaena hippurus* (Coryphaenidae) from Peru

The dolphin fish, *Coryphaena hippurus*, is found worldwide in warmer seas (Miller and Lea 1976). Little information is available on its reproductive biology. Beardsley (1967) analyzed seasonal gonadal changes in *C. hippurus* in the Florida current. Other papers (Schuck 1951; Erdman 1956; Williams and Newell 1957; Gibbs and Collette 1959) reported observations of spawning. Schweigger (1964) concluded that this species spawns in Peru during March. Here we present a histological analysis of the gonads of 43 female *C. hippurus* from northern Peru.

Fish were collected 4 June 1983 from Huarmay, Ancash Department, Peru (lat. 10°04'S, long. 78°10'W) by commercial fishermen. Landings of *C. hippurus* by Peruvian fishermen are not common. Their presence in 1983 was due to the "El Niño" phenomenon during which time warm oceanic waters were found along the Peruvian coast. Our sample therefore, was probably from a tropical population that followed a warm water mass southward. During normal years, the population presumably would be located further north. Fish were shipped on ice to Trujillo, La libertad Department, Peru where we weighed them to the nearest kg using a spring balance, weighed gonads to the nearest g using a torsion balance and fixed gonads in 10% formalin 5 June 1983. Tissue was embedded in paraffin. Ovarian histological sections were cut at 8 μ m and stained with Harris' hematoxylin followed by eosin counterstain. Gonosomatic indices ($GSI = \text{ovary weight/fish weight} \times 100$) (Table 1) were calculated.

The following classification scheme was used for the ovaries (sizes are mean diameters): regressed, primary oocytes (93 μ m) predominate; previtellogenic, vacuolated oocytes (155 μ m) present; vitellogenic, yolk deposition in progress in enlarging follicles (334 μ m); spawning condition, mode of mature oocytes (608 μ m) present containing an enlarged zona radiata. We divided our sample into size groups according to this classification scheme (Table 1).

The dolphin fish is a multiple spawning fish as we observed more than one stage of eggs in the same ovary with evidence of reproductive activity (mature or vitellogenic eggs). Beardsley (1967) also reported that *C. hippurus* spawn more than once during a single spawning season. We did not determine the minimum size for sexual maturity. However, because the smallest female in our sample was in spawning condition, all were classified as adults. This fish measured 66 cm standard length (SL). Twenty two of our sample of 43 females were in spawning condition (Table 1). Five of these females contained postovulatory follicles. These structures are evidence of a recent spawning as they are derived from the granulosa cells of the spawned egg. Postovulatory follicles of *C. hippurus* are convoluted structures and contain an irregularly shaped lumen lined by cuboidal epithelium and an underlying connective tissue theca. Their longevity in teleost fishes is brief. Hunter and Goldberg (1980) found they were detectable for less than 48 hours after spawning in the northern anchovy, *Engraulis mordax*. Thus, 11.6% of our total sample had spawned on or around 3 June 1983.

Another worker (Beardsley 1967) reported a long spawning season (November–

Table 1. Distribution of body sizes (standard lengths), gonosomatic indices ($\pm$ SE) and spawning cycle stages for 43 Peruvian *Coryphaena hippurus* collected 4 June 1983.

N	Standard lengths (range, cm)	Gonosomatic indices	Regressed (%)	Previtellogenic (%)	Vitellogenic (%)	Spawning (%)
3	66–77	3.13 $\pm$ 1.80	0	0	0	100
24	78–89	1.95 $\pm$ 0.26	0	37	17	46
16	90–102	1.92 $\pm$ 0.27	6	25	19	50

July) with a March peak for *C. hippurus* in the Florida current. Gibbs and Collette (1959) found young *C. hippurus* at all seasons of the year in the Florida current but at peak abundance during the summer. Thus, a long spawning season would be reasonable for this species in Peru. Schweigiger (1964) reported *C. hippurus* spawn in Peru during March. Gonads from April were spent. However, he did not examine gonads on a seasonal basis so we cannot infer the duration of the cycle from his data.

It is impossible to characterize the entire spawning cycle from a single sample. Nevertheless, the occurrence of almost half the sample in the previtellogenic and vitellogenic condition (Table 1) suggests it was collected early in the spawning cycle when part of the population contained ripening ovaries. One might therefore expect the peak of spawning to be several months later, perhaps August–September. Were peak spawning of Peruvian *C. hippurus* to occur at this time (early spring in southern hemisphere) this would approximate the time (by season) designated for maximum spawning in this species by Beardsley (1967).

Acknowledgment

We thank Jorge Oliva Nuñez for assistance in mensuration.

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Flight Period, Range Extension, and Variability of *Heteranthidium autumnale* Snelling (Hymenoptera: Megachilidae)

There are published records for three specimens of *Heteranthidium autumnale*: the male holotype and female allotype from Desert Hot Springs, Riverside County, California, 8 November 1963 (Snelling 1966), and a second male from Rancho Buena Vista, Baja California Sur, Mexico, 16 October 1972 (Snelling 1975). Since then, a third male was taken on *Antigonon leptopus* Hooker and Arnott (=Cor-alvine), 9.6 miles north of Loreto, Baja California Sur, Mexico, 14 September 1983, by Roy R. Snelling. On 14 October 1983, Mr. Jack Hall (of the Department of Entomology, University of California, Riverside) and I collected 4 ♀♀ and 1 ♂ of this species at Vidal Wash in eastern Riverside County. On 17 October I returned and took an additional 4 ♀♀ and 5 ♂♂. Flowering was extremely scanty about and at the wash, and both male and female *H. autumnale* were collected exclusively on the flowers of *Bebbia juncea* (Benth.) Greene, near the close of their bloom, growing in widely scattered patches along a half kilometer of the wash. Somewhat fewer clumps of *Encelia frutescens* Gray were also present, but their flowers were visited by relatively few insects and no megachilids.

Only two other species of megachilid were taken on those two days at Vidal Wash, both from *Bebbia* and from which the females were collecting pollen, like those of *H. autumnale*. They were a species of *Megachile* (*Xeromegachile*) (16 ♀♀, 1 ♂), and a single male dark-winged *Heterostelis* (11.6 mm body length, 8.5 mm fore-wing length) markedly distinct from all hitherto described males of *Heterostelis* (Thorpe 1966) and, quite probably, a species parasitic upon *H. autumnale*.

Only one of the females of *H. autumnale* had slightly worn mandibles (a blunting of the acute tooth at the posterior angle of the mandible), all individuals possessed unfrayed wings and bright liveries, and males and females were about equally frequent. The bees were thus still in their early flight period, but probably not at its onset. In contrast the female allotype has very worn mandibles, with both the middle and basal tooth wholly eroded (fig. 1G, Snelling 1966).

The known flight period of *H. autumnale* in California therefore includes the span from 14 October-6 November, overlapping and extending that in Lower California (14 September-16 October). As the Rancho Buena Vista locality is some 1770 km SSE of Desert Hot Springs and something over 1660 km S by E of Vidal (in turn 600 km ENE from Desert Hot Springs), it is likely that *H. autumnale*, the least well-known of larger California anthidiines, will be found to be wide-spread, perhaps patchily distributed, at lower elevations, further to the north as well, frequenting *Bebbia*, and perhaps other composites, in desert washes and canyons of California from late September to mid-November.

The series of 14 fresh specimens permits a broader view of variation and morphological characteristics in *H. autumnale*. Coloration is markedly variable, as in *H. zebratum* (Cresson), and on average the six males corresponded more

closely with that from Lower California (Snelling 1975). The only maculations regularly in agreement with the description of the male holotype are those of the mandibles, labrum, clypeus, lateral facial marks, underside of scape, irregular stripe across vertex, mesoscutal stripes adjacent to the tegulae, a spot on the tegulae (but not always comma-shaped), a minute spot on the axillae, and a submedian pair of spots on the mesoscutellum; all other coloration is of many patterns, including that of the metasoma, except for tergite VI which is largely yellow, with a lateral spot on each side. The darker colors of the legs range from piceous to ferrugineous. All of the specimens, both male and female, have a medial ferrugineous area (from small to very large) on the anterior face of the first metasomal tergite.

Significant structural features of males include: 5–6 (6 in two specimens) low rounded denticles on the unworn anterior margin of the clypeus (3 in the holotype), with pencils of yellow hairs projecting from the interspaces; mandibles 3-dentate, tooth at basal angle acute, prominent, about 1.5 times height of, and separation from, the low apically directed, obliquely rounded medial tooth adherent to the base of apical tooth; a raised, multidentate (1–5 denticles per side, $\bar{m} = 3.4$ per side) eminence at each postero-lateral margin of the median apical emargination of metasomal sternite V, the carinae and tubercle within the depressed area variously developed; male intromittant organ with an eversible sac containing a medial pair of large brown sclerites on its dorsal wall; ventral lobe of gonocoxite broader than earlier portrayed, not abruptly incised along proximal lateral margin but broadly, shallowly incurved (cf. fig. 1E [legend reversed], Snelling 1966).

Maculation of the female is only slightly less variable; individual spots frequently unite (as on the mesoscutum), or stripes or color fields are broken into isolated spots (as that behind the upper third of the eye, or the butterfly-shaped macula on tergite VI; or the ground color may differ—in most cases that of the legs is ferrugineous). Those maculae regularly in agreement with the description of the female allotype include that on the clypeus, the lateral triangular facial marks, the stripe across the summit of the vertex, that on the tegulae, and the basal spots on all tibiae; all else varied, including the metasomal patterns. For some characters no specimen resembles the female allotype (e.g., none has an “obscure spot” on the anterior corner of a pronotal lobe, or a long yellow stripe on tibiae-1, etc.). Scopa amber colored medially or throughout in 4 specimens, medially ferrugineous in only 2.

Structural features of females include strongly tridentate mandibles, with the tooth at the inner angle acute (mandibles greatly worn in the allotype); anterior margin of clypeus not evenly curved but, as in other members of the *zebratus* complex, perceptibly crenulate, with hair tufts emanating from each of the insinuations (of which there are 5–8, $\bar{m} = 6.1$); anterior, apical strigular comb with 6–10 tines ($\bar{m} = 8.2$); mid-basitarsus 2.9–3.3 ($\bar{m} = 3.1$) times longer than broad, 0.65–0.68 ($\bar{m} = 0.66$) times as long as hind basitarsus; hind basitarsus 2.4–2.85 ($\bar{m} = 2.6$) as long as broad, about 0.67–0.81 ($\bar{m} = 0.74$) times as long as hind femur; metasomal tergite VI with a sharply defined, deep marginal sulcus, with a slight medial emargination on its ventral rim.

As Snelling says, both sexes of *H. autumnale* may be separated from other species by having the anterior coxa postero-medially prolonged as a spine (less obvious, blunter in ♂), plus a high sharp carina on the pronotal lobes and immaculate mesopleurae.

Acknowledgments

I am grateful to Roy R. Snelling for his comments, as well as for the new record, so generously proffered, of a male from Lower California, and to my wife, Dr. Ruth S. Cooper, for help in the field and identification of plants.

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COVER: A sphinx moth caterpillar, *Hemeroplanes ornatus*, from the Iquitos area, Peru. The snake pattern mimics *Bothrops delineatus*, but is upside down on the caterpillar. Photograph by George Dodge. Submitted by Charles Hogue, Curator of Entomology, Natural History Museum of Los Angeles County.